THE FOSSIL CRAB

OMMATOCARCINUS CORIOENSIS (CRESSWELL)

and a review of related Australasian species

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Summary

Ommatocarcinus corioensis (Cresswell), distinctive for its elongate eyestalks and chelipeds, occurs widely in the marine Lower Miocene to Pliocene of southeastern Australia and is particularly abundant in the late Lower and Middle Miocene. It is apparently ancestral to the extant Australian *O. macgillivrayi* White, both being characterized by a pterygostomial stridulating ridge. Regression analyses show that in each the growth of the male chelae is positively allometric with respect to the carapace. The living New Zealand *O. huttoni* Filhol, which lacks a pterygostomial stridulating ridge, evidently represents a separate lineage.

O. corioensis occurs in association with fossil burrow complexes which closely resemble the dwelling burrows of its extant, European, near-relative *Goneplax rhomboides* (Linné). It was a neritic species; its times of greatest abundance relate to oxygen isotope temperatures of 14 to 17° C and the prevalent deposition of relatively fine grained sediments favourable to its burrowing habits.

Fossil species of *Ommatocarcinus* White occur in the Middle Eocene of Spain and the Neogene of Australia and New Zealand. Extant species are found in the Indo-West Pacific region, including Natal. The genus is considered ancestral to *Goneplax* Leach.

Introduction

Cresswell (1886) gave a short description of a fossil crab he named *Gonoplax corioensis,* obtained from nodules collected at Curlewis and North Shore near Geelong, Victoria. Hall (1905) redescribed the species and correctly referred it to the genus *Ommatocarcinus* White. While Hall's description is sufficiently detailed to characterize the species, it fails to describe the ventral parts of the crab, says little about the ambulatory legs, and is inadequate for the identification of the very fragmentary remains frequently encountered.

Since the time of Hall's description numerous new specimens of the fossil crab, some unusually well preserved and remarkably complete, have been obtained from a variety of localities. In the same period, studies by many workers have greatly increased knowledge of the Tertiary stratigraphy of southern Australia. This paper aims to provide a detailed description of *O. corioensis* and to analyze its systematic position relative to the other described species of *Ommatocarcinus,* particularly the living Australian *O. macgillivrayi* White, 1852. The stratigraphic distribution of *O. corioensis* is reviewed in the light of the new finds, and information concerning its palaeoecology is presented.

The available descriptions of *O. macgillivrayi* omit details of potential diagnostic significance and in an attempt to correct this a new description is provided. New illustrative material and also a diagnosis are given for the extant New Zealand *O. huttoni* Filhol, 1885, which was recently redescribed by Takeda and Miyake (1969).

The depositories of the fossil and recent materials studied are as follows:

National Museum of Victoria, Melbourne, Victoria (N.M.V.).

Geology Department collection, The University of Tasmania, Hobart, Tasmania (T.U.).

Palaeontological collection, Department of Geology and Mineralogy, The University of Adelaide, Adelaide, South Australia (A.U.).

The Australian Museum, Sydney, New South Wales (A.M.).

The Queensland Museum, Brisbane, Queensland (Q.M.).

Dominion Museum, Wellington, New Zealand (D.M.).

Systematics

Order Decapoda

Family Goneplacidae MacLeay, 1838

Subfamily Goneplacinae MacLeay, 1838

Genus OMMATOCARCINUS White, 1852.

Ommatocarcinus White, 1852: 393. H. Milne-
Edwards, 1852: 163. Miers, 1886: 246. Stebbing,
1893: 92. Alcock, 1900: 280, 293. Tesch, 1918:
181, 186. Barnard, 1950: 282, 285. Glaessner,
1960: 28; 1969: R525. Bennett, 1964: 74. Guinot,
1969: 523. Takeda and Miyake, 1969: 173-175.
Vía, 1970: 310-311, 314-316.
Neommatocarcinus Takeda and Miyake, 1969: 173-
175.
Glaessneria Takeda and Miyake, 1969: 175.
(non) *Glaessneria* Wright and Collins, 1972: 34.
Type species: *Ommatocarcinus macgillivrayi* White,
1852, by monotypy.

Diagnosis

Carapace trapezoidal or pentagonal, its
width between tips of large, single extraorbital
spines more than 1·6 times length; front nar-
row, less than 1/4 width of carapace between
tips of extraorbital spines, usually deflexed and
more or less truncate; inner-orbital notches
generally well indented; orbits elongated trans-
versely, trough-like to accommodate greatly
elongated eyestalks; extraorbital spines usually
directed laterally; pterygostomial regions with
an anterior ridge which may or may not be
transversely ribbed for stridulating. Basal three
segments of male abdomen occupying all of
width between coxa of last pereiopods or re-
duced in width. Chelipeds, particularly those
of males, usually sub-equal and strongly
elongated, with palms compressed and fingers
elongate. Ambulatory legs slender.

Remarks

Miers (1886) considered *Ommatocarcinus*
closely allied to *Goneplax* Leach. Both genera
are characterized by having the frontoorbital
margin the widest or nearly the widest part of
the carapace, the orbits trough-like for accom-
modating greatly elongated eyestalks, the
anterolateral angles produced to a spine, and
the chelipeds elongated. Tesch (1918) and
Bennett (1964) indicated that some members
of both genera have the basal segments of the
male abdomen reduced in width, not occupying
the full distance between the coxa of the last
pair of legs as suggested by Miers.

Ommatocarcinus differs from *Goneplax* in
having a relatively narrower front which gene-
rally has well defined inner-orbital notches.
The more typical forms of *Ommatocarcinus*
have the extraorbital spines strongly produced
and directed laterally, not short and forwardly
directed as in *Goneplax*. Apparently no mem-
bers of *Goneplax* have a stridulating device.

Takeda and Miyake (1969) split *Ommato-
carcinus* into *Ommatocarcinus* White and two
new genera, *Neommatocarcinus* (type species
O. huttoni Filhol, 1885) and the monotypic
Glaessneria (type species the fossil form *O.
arenicola* Glaessner, 1960). *Neommatocarcinus*
is distinguished from *Ommatocarcinus* on the
basis of details of its sub-frontal features and
antennules, the form of its buccal cavern and
third maxilliped, the absence of a pterygo-
stomial stridulating ridge, and most importantly,
the form of the male abdomen, which is nar-
rowed with several segments fused. The fossil
form *O. zariquieyi* Vía, 1959, from the Eocene
of Spain, is also referred to *Neommatocarcinus*
because it shows a similar fusion of abdominal
segments.

O. macgillivrayi and *O. huttoni* are herein
compared in plate IV. A number of the differ-
ences on which Takeda and Miyake base
Neommatocarcinus are quite minor, notably
the lengths of the antennules and variation in
the maxillipeds. The high crest on the epistome
of *O. huttoni* is an exaggeration of the same
feature in *O. macgillivrayi*. The development
of stridulating devices may be variable amongst
species of a single genus such as in *Ovalipes*
Rathbun (Stephenson and Rees, 1968; Stephen-
son, 1969). Crabs show a persistent evolution-
ary trend towards reduction of the abdomen
(Glaessner, 1960) and such simple evolutionary
steps as the narrowing and fusion of abdominal
segments might potentially occur in a number
of quite separate species lineages. Thus while
the differences between *O. macgillivrayi* and
O. huttoni are of undoubted significance at the
species level, there seems little real justification
for a generic separation which leads only to a
proliferation of names in the literature.

O. arenicola, the type of *Glaessneria,* is
known only from a single mould lacking detail,
and at the present very imperfect state of

knowledge concerning it, referral to a new genus seems quite unwarranted. Takeda and Miyake claim that the "contour" of its carapace is distinctive, but this feature is quite variable in the goneplacid genus *Carcinoplax* H. Milne-Edwards (Imaizumi, 1961). In the outline of its carapace *O. arenicola* resembles *O. fibriophthalmus* Yokoya, 1933, and there seems no obvious reason to preclude it from *Ommatocarcinus*.

Ommatocarcinus corioensis (Cresswell, 1886)

Fig. 1A-E, Fig. 7A,B, Fig. 9, Pl. 4 figs. 1-8, Pl. 5 figs. 1a-10.

Gonoplax corioensis Cresswell, 1886: 90, 91.
Ommatocarcinus corioensis (Cresswell) Hall, 1905: 356-360, pl. 23, figs. 1-5. Chapman, 1914: 247, fig. 120B. Glaessner, 1960: 29, fig. 12c; 1969: R525, fig. 334. Takeda and Miyake, 1969: 175. Via, 1970: 314.

Diagnosis

Carapace trapezoidal with two transverse ridges; anterior margin of front gently sinuous, slightly concave on either side of a median convexity; supraorbital margins with inner part acute and outer part subrounded in profile, a row of spinules along the whole length; extraorbital spines laterally directed, strongly produced, and narrow based; well developed anterolateral rises, coarsely granulate. Basal segment of eyestalks concealed. Pterygostomial regions with a stridulating ridge bearing numerous short transverse striae. Male abdomen seven-segmented; first three segments just reaching coxae of last pereiopods. Mature cheliped meri with a basal stridulating plectrum, an evenly spaced row of spinules on anterior margin, three spinules on distal part of ventral margin, and a spinule half way along dorsal margin.

Material

Over one hundred and seventy specimens, including the types in the National Museum of Victoria, were examined.

The lectotype, here designated as N.M.V. No. P7665, is in a water-rounded phosphatic nodule collected by the Rev. A. W. Cresswell at Curlewis near Geelong, Victoria. Specimen N.M.V. No. P7666, also in a nodule collected by Cresswell at Curlewis, is designated a paralectotype.

Three hypotypes of Hall (1905), ♂, N.M.V. No. P7667, ♀ N.M.V. No. P7668, N.M.V. No. P7669, are from (the Port Campbell Limestone) Two Mile Beach, Port Campbell, Victoria.

Occurrence and Stratigraphic Position

This species is known from numerous widely distributed localities in southeastern Australia (including Tasmania) and also from the upper part of the continental slope off northern New South Wales. Its occurrence is outlined in detail in a following section of this work entitled 'Preservation and stratigraphic distribution of *O. corioensis*', pp. 48-52.

Age

Lower Miocene to Pliocene, particularly common in the late Lower Miocene and Middle Miocene.

Description

The trapezoidal carapace is widest from tip to tip of the strongly produced, laterally directed extraorbital spines; the dorsal surface is slightly arched transversely, but sagitally slopes moderately down to the anterior and posterior from a flattish transverse median area.

The front is deflexed and narrow, between one sixth and one seventh the width of the carapace between the tips of the extraorbital spines; its anterior margin is almost straight except for a gentle concavity on either side of a slight median convexity. The front has a border which is very narrow on the anterior margin, but considerably wider adjacent to the inner-orbital notches where it bears a shallow groove containing a row of pits.

The supraorbital margins slant rearwards a little, are slightly convex at the innermost part, but otherwise nearly straight; they bear a single row of spinules. The spinules are short and close-spaced on the acute inner third of each supraorbital margin, but become longer and more widely spaced on the outer two thirds, which is subrounded.

The extraorbital spines are narrow based

with their hind margin rather abruptly curving to the lateral regions of the carapace. The hepatic regions and the upper surface of the extraorbital spines bear distinct granules.

The nearly vertical anterolateral regions are anterior to distinct lateral rises which are directed slightly upwards and densely covered by coarse granules. The postero-lateral regions slope steeply downwards and outwards to meet the pleural sutures of the carapace and are markedly convergent rearwards. The slightly concave posterior margin has a prominent posterior border.

The carapace is divided dorsally into three subequal flattish parts by a distinct ridge extending between the lateral rises, and a shorter ridge arched towards the anterior over the front of the cardiac region. The ends of the anterior ridge curve posteriorly, its central part is pitted and the distal ends bear small granules. Two depressions lie just anterior to the curve of the ridge and a third depression notches it near its termination.

Most of the regions on the dorsal part of the carapace are slightly tumid and are separated by shallow grooves. The mesogastric region is raised, sub-triangular, with an anterior prolongation. The urogastric region is depressed and constricted; it is delimited laterally by deep grooves which are convex inwards. The cardiac region is trapezoidal, widest anteriorly. The intestinal region is gently arched; its antero-lateral extent is marked by broad depressions. Distinct longitundinal crests are formed at the junction of the dorsal mesobranchial regions and the sloping posterolateral regions. These crests converge slightly towards the posterior and bear distinct oval tubercles, elongate in a transverse direction. The outer part of the branchiocardiac furrow is broad and shallowly depressed; the inner part consists of several depressions, the most marked of which is the deep curved groove at the side of the urogastric region.

Most of the dorsal surface of the carapace is minutely granulated; there is a gradation into the regions of coarse granules described above. The posterior border is smooth. Depressions and pits on the exterior of the carapace correspond to muscle attachments on the interior surface (Fig. 1C).

The orbits form long narrow trenches; they open to the subfrontal region via notches containing the antennal bases. The suborbital margins are concave except for the innermost part which projects bluntly forwards and curves downwards just lateral to the notch for the antennae. The inner two thirds of each suborbital margin have an acute profile and one line of more or less distinct granules.

The eyestalks (one only shown, Fig. 1A) are slender and elongate with the base of the corneae apparently a little beyond the tips of the extraorbital spines. The base is expanded; the first segment is not exposed.

The antennule bases lie close together near the subfrontal median septum which is shaped like an inverted 'Y'. The epistome is wide with the hind margin mainly concave except for a small central projection and a slight notch half way between the centre and the lateral margin.

A curved stridulating ridge with about 76 transverse ribs is situated on the anterior part of the pterygostomial region. The buccal frame is more broad than long with the sides nearly parallel.

The ischium of the third maxilliped (Fig. 1D) is as broad as it is long, convex inwards, concave exteriorly, and with a prominent basal projection directed laterally. The merus is sub-quadrate, wider than long, with the lateral anterior angle abruptly rounded. The palp is imperfectly known. The exopodite is gently arched inwards and reaches a little more than the middle of the merus; there is a small lateral projection at the base.

The sternum is somewhat rounded, broader than long, with the posterior straight. The anterior segment is large, broad, and sub-pentagonal with the posterior an obtuse angle. The second and third segments are subequal, the fourth is half as long again as each of the second and third segments, and the fifth is reduced. The first four segments have crescentic episterna extending back adjacent to the next posterior sternite and forming the anterior boundary of the socket for the coxa of the limb
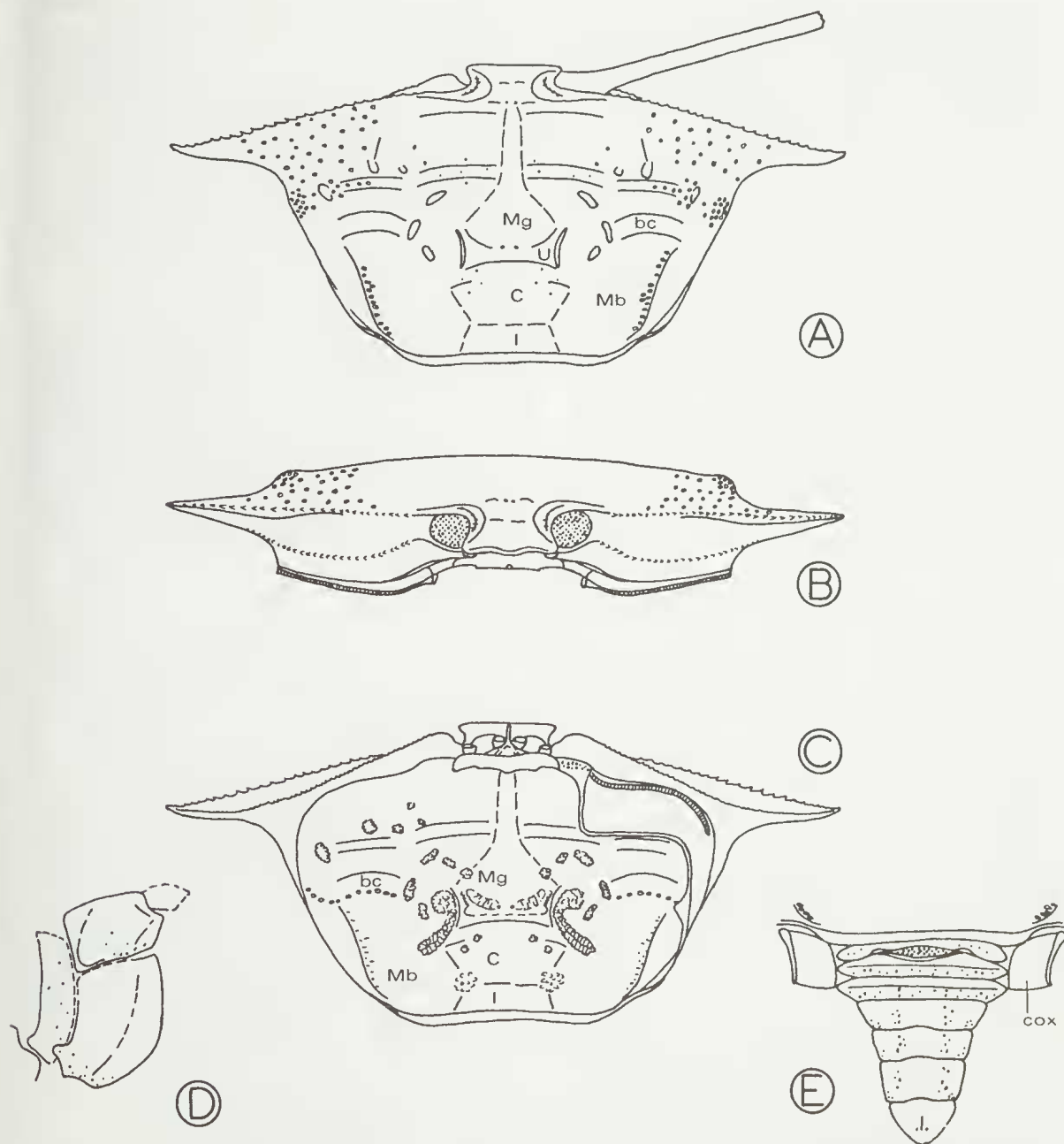
FIGURE 1

Ommatocarcinus corioensis (Cresswell)

A-C, reconstruction of carapace. A, dorsal view with regions of carapace lettered; Mg, mesogastric; U, urogastric; C, cardiac; I, intestinal; Mb, meso-branchial; bc, branchiocardiac furrow. B, anterior view. C, ventral view with right pterygostomial-brachiostegal plate removed. All x 1½. D, reconstruction of right third maxilliped, ventral view: x 3. E, reconstruction of male abdomen; cox, coxa of fifth pereiopod: x 1½.

of the next somite. The surface of the sternum is sparsely pitted.

The abdomen is in seven segments; the three basal segments extend the full distance between the coxae of the last pereiopods in mature individuals of both sexes. The first three segments of the male abdomen (Fig. 1E) have the lateral portions tapered and rounded; later segments are progressively narrow towards the rounded, triangular telson. The female abdomen has the lateral portions of the second and third segments rounded, the fourth to sixth segments decreasing only slightly in width, and the telson broad and semi-circular.

The chelipeds are elongate and sub-equal. The short coxae are pitted near the ventral, distal margin. The ischia have an anterior ridge which is produced and expanded distally to a blunt proturberance. The meri are narrow, elongate, slightly arched towards the anterior, and have a rounded-triangular cross-section with the dorsal and ventral margins distinctly granulated. On the proximal dorsal part of the meri, just anterior to a basal V-shaped suture, three small ridges are opposed to the pterygostomial stridulating ridge. Nine to twelve evenly spaced spinules are situated on the anterior margin, one short blunt spine is midway along the dorsal, and three spinules are positioned on the distal part of the ventral margin of each merus. The carpi are globular, with a short anterior border, a stout internal spine and an external spinule. The marginal areas are granulated. The palms are compressed, and widest between the rounded dorsal and ventral margins. A slight sulcus is on the ventral part of the outer face, and the inner face has a broad longitudinal ridge. The dorsal and ventral margins and the ridge on the inner face are distinctly granulated; a line of several spiniform granules is on the distal part of the inner face near the dorsal margin. The fingers are elongate, curved and somewhat laterally compressed with shallow, median, longitudinal grooves. The prehensile margins have subtriangular or rounded teeth. Rows of pits are situated near the teeth and in the median, longitudinal grooves.

In large males the extended length of one cheliped may be nearly twice the width of the carapace between the tips of the extraorbital spines. The palms are rather narrow, but broaden distally where the ventral margin is compressed. The right palm is slightly broader than the left; there is a slight gap between the bases of the right fingers, but none between the left. The proximal teeth on the right fingers are rounded; the distal teeth are acute. On the left fingers the teeth are separated and acute with sharp margins. The finger tips of both hands are curved to form pincers.

The chelipeds of the female are shorter than those of the male. The palms are relatively broader and shorter with the ventral margin straight or gently convex and compressed. The right fingers are hardly separated at the base, but the proximal teeth are rounded as in the male. The teeth of the left fingers are not separated. Terminal pincers are not well developed on the fingers of either hand.

The ambulatory legs increase in length in the order 1, 4, 2, 3. The longest is about one and a quarter times the width of the carapace between the tips of the extraorbital spines. The coxae are sub-quadrate with a row of pits on the ventral, distal margin. The meri are compressed and fusiform, widest medially, and about a quarter as wide as long; the outer half of the dorsal margin is finely granulated and bears one to three distal spinules. The carpi are half the length of the meri; they are arched dorsally and widened distally with the distal part of the dorsal margin produced to form a broad spine. The propodi are compressed and about a quarter as long again as the carpi; they taper slightly and the faces have a longitudinal groove containing several pits. The ventral margins of the propodi of the first and second pairs of legs have a line of pits which probably contained hairs in life. The dactyli are long, curved and tapering with two dorsal longitudinal grooves containing elongate pits.

Several specimens show traces of coloration; the palms are speckled with grey and the tips of the fingers of males are dark coloured.

Dimensions

Measurements are given in Table 1 for three nearly complete skeletons and one other showing the third maxillipeds.

Regression Analysis

Regression analyses have been made on measurements from two collections:

(a) Male specimens from the late Lower Miocene and Middle Miocene sediments, and the late Miocene or Pliocene phosphatic nodule beds of the Otway Basin, Victoria.

(b) Male specimens of late Lower Miocene age from the upper member of the Morgan Limestone near Morgan in the South Australian portion of the Murray Basin.

For both these collections analyses were made of the relationships between the length of the cheliped palms and the width of the carapace just behind the base of the extraorbital spines, and between the length of the cheliped palms and their width. For the numerically larger Victorian collection an analysis was also made of the relationship between the length of the carapace and its width just behind the base of the extraorbital spines. The original data and their analyses are presented in scatter diagrams, Fig. 2A-C, and Table 2.

For the Victorian males the value of the coefficient of correlation, r, is close to unity for the distribution of X_1, Y_1, but is rather less for the distributions of X_1, Y_2 and X_2, Y_2 (Table 2). The collection is thus rather variable with respect to the dimensions of the chelipeds. The values of 'r' are still fairly high in every case and so indicate a marked linearity in the distribution of each of the three sets of data analysed. The slope of the regression lines indicates that the growth relationship between the length of the carapace and its width is not quite isometric, and the lengthwise growth of the cheliped palms is positively allometric with respect to their width and the width of the carapace (Fig. 2A).

TABLE 1

Dimensions of *Ommatocarcinus corioensis* in millimetres

The method of measuring for this and the other species described follows that of Rathbun (1918). The measured specimens are: ♂ from the Port Campbell Limestone at Gravel Point. S.E. of Port Campbell, Victoria, N.M.V. P24721; ♂ from the Port Campbell Limestone, above the notch E. of the Amphitheatre near Port Campbell, N.M.V. P24719; ♀ from the Fyansford Clay, in the left bank of the Barwon River at Section 2B, Parish of Murgheboluc, Victoria, N.M.V. P25987.

	♂, N.M.V. P24721	♂, N.M.V. P24719	♀, N.M.V. P25987
Width of carapace between tips of extraorbital spines	58 (impf.)	54	38 (impf.)
Width of carapace just behind bases of extraorbital spines	43	38	29
Length of carapace	27	24	18
Greatest width of front	8·6	7·4	5·4
Length of palm of right cheliped	—	43	16
Length of palm of left cheliped	51	—	18
Width of palm of right cheliped	—	13	—
Length of right fixed finger	—	16	—
Length of left fixed finger	—	16	—

Lengths of ambulatory appendages of ♂, N.M.V. P24721

	Coxa + basis	Ischium	Merus	Carpus	Propodus	Dactylus
First	—	—	25 (impf.)	10	12	12 (impf.)
Second	—	—	28 (impf.)	12	15	11 (impf.)
Third	—	—	29	12	15	12
Fourth	4·7	2·2	25	12	12	12

Total length from merus to dactylus inclusive

First	59
Second	66
Third	68
Fourth	61

For the Morgan male crabs the slope of the regression lines (Fig. 2C and D) indicates that the lengthwise growth of the cheliped palms is again positively allometric relative to the width of the carapace. The allometry is, however, markedly less than for the Victorian specimens.

Examination of the limited data for Victorian females on Fig. 2B and C suggests that the increase in length of the palms is nearly isometric with respect to their width and to the growth of the carapace. The data for one Morgan female is similar to that for the Victorian females.

Remarks

Cresswell (1886) incorrectly described the eyestalks as being comparatively short and the second pair of ambulatory legs as the longest. Hall (1905) corrected the first error but gave little detail concerning the legs. Hall's work also contains several errors; he describes the 'anterior edge' of the carapace as finely and regularly granulated and the cardiac area as triangular. In the lectotype the spinules on the supraorbital margins are largely covered by sediment or broken and the cardiac region is damaged by a V-shaped fracture. Hall also incorrectly states in his remarks that there is no spinule in the middle of the dorsal margin of the cheliped meri.

Usually, large males have the right chela the major. In approximately one in five specimens the heterochely is reversed. One specimen, A.U. F17220, in a phosphate nodule from 'Coghills' near Geelong, Victoria, has the left cheliped about half the size of the right. This may be an example of regeneration.

The male crabs from Morgan differ from most of the Victorian males in having somewhat shorter and broader chelipeds. However, several males from Victoria also have short, broad chelipeds. A gradational series appears to exist between the Victoria crabs with long chelipeds and the Morgan specimens. It is thus considered impracticable to separate the two forms. The differences in the chelipeds are shown in the regression analyses.

Ommatocarcinus macgillivrayi White, 1852

Fig. 9; Pl. 5 Fig. 11, Pl. 6 Figs. 1-3, Pl. 7 Figs. 1, 2a-e.

Ommatocarcinus macgillivrayi White, 1852: 393-394, pl. 5, figs. 1, 1a. H. Milne-Edwards, 1852: 163. Haswell, 1882: 90-91. Balss, 1922: 138. Sakai, 1934: 314, fig. 22; 1936: 137, fig. 96; 1939: 564, pl. 102, fig. 5; 1965: 170, pl. 84, fig. 3. Guinot-Dumortier and Dumortier, 1960: 121, figs. 3, 3a. Glaessner, 1960: 29, fig. 12d. Guinot-Dumortier, 1961: 83, fig. 5. Griffin and Campbell, 1969: 151-153, figs. 4, 6D. Guinot, 1969: 523, figs. 69-70. Takeda and Miyake, 1969: 174. Vía, 1970: 314.
Ommatocarcinus sp. Yokoya, 1933: 198-199, fig. 65A, B.
Ommatocarcinus pulcher Barnard, 1950: 286, fig. 53b-f.
(non) *Ommatocarcinus macgillivrayi* Miers, 1886: 247-248 (= *Ommatocarcinus huttoni* Filhol, 1885).

TABLE 2

Analyses of data indicated on the scatter diagrams comprising Figure 2. The variables are as explained in the legend of Figure 2.

| Number of Items of Data	Variables	Coefficient of Correlation r	Equations of Regression Lines	Standard Errors for Regression Coefficients		Standard Errors of Estimate	
				Syx	Sxy	Sy	Sx
20	X_1, Y_1	·98	$Y_1 = \cdot 91X_1 - \cdot 069$ $X_1 = 1 \cdot 05Y_1 + \cdot 14$	·029	·033	·0016	·0017
23	X_1, Y_2	·88	$Y_2 = 1 \cdot 73X_1 - 1 \cdot 14$ $X_1 = \cdot 45Y_2 + \cdot 85$	·20	·052	·091	·045
19	X_2, Y_2	·91	$Y_2 = 1 \cdot 45X_2 - \cdot 003$ $X_2 = \cdot 57Y_2 + \cdot 19$	·16	·064	·083	·052
7	X'_1, Y'	·94	$Y' = 1 \cdot 43X'_1 - \cdot 78$ $X'_1 = \cdot 62Y' + \cdot 66$	·24	·10	·055	·036
14	X'_2, Y'	·96	$Y' = 1 \cdot 16X'_2 + \cdot 15$ $X'_2 = \cdot 79Y' - \cdot 028$	·10	·069	·050	·041
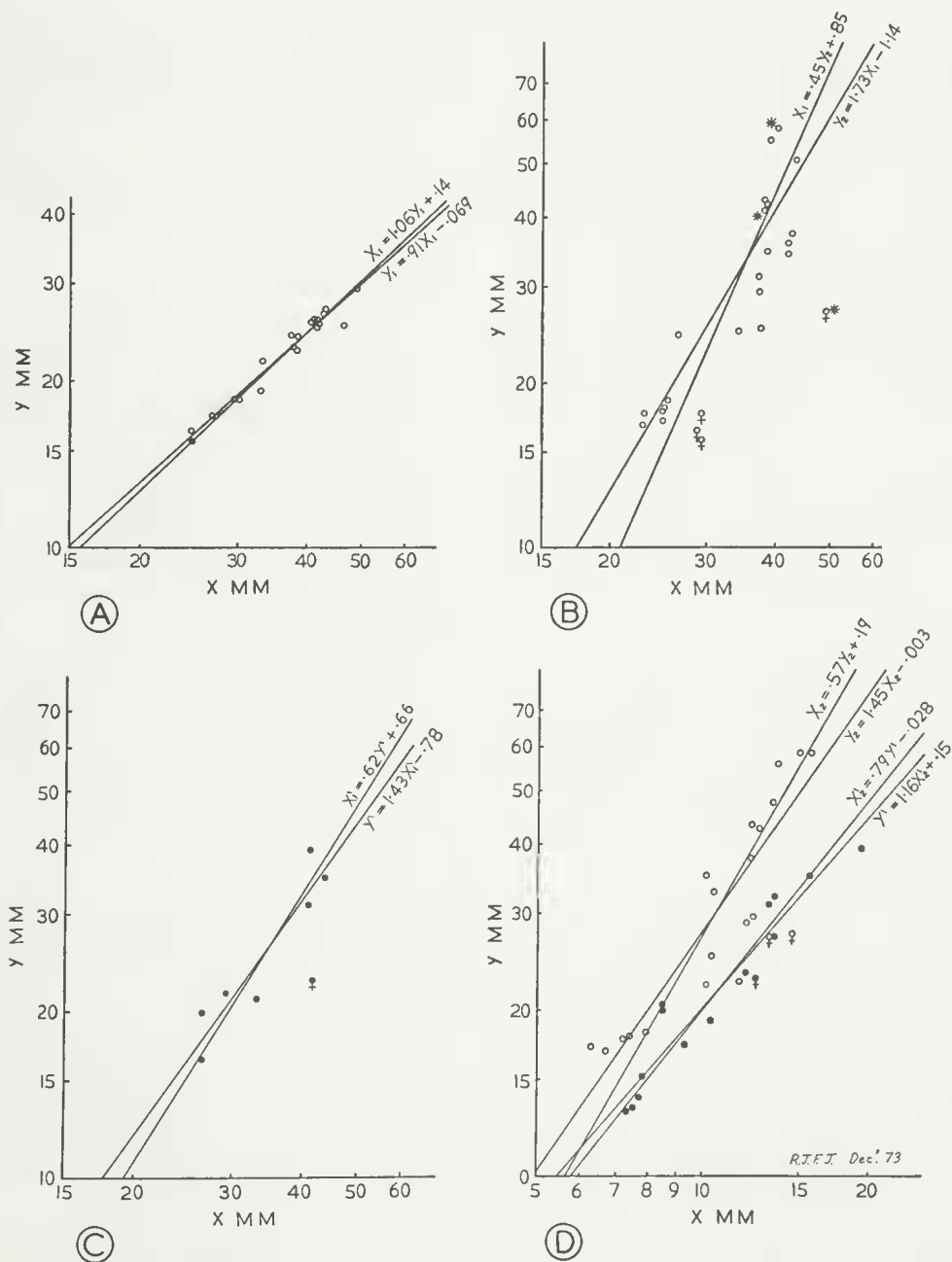
FIGURE 2

Regression analyses for selected dimensions of male specimens of *O. corioensis*.

A: Victorian collection; log width of carapace just behind extraorbital spines, X_1, on log carapace length, Y_1, data $\bigcirc$.

B: Victorian collection; X_1 on log length of cheliped palm, Y_2, data $\bigcirc$. Coincident data indicated by an asterisk. Female data shown ♀, but not included in regression analyses.

C: Morgan collection; log width of carapace just behind extraorbital spines, X'_1, on log length of cheliped palm Y', data ●. Female data, ♀, not included in analyses.

D: Victorian collection; log width of cheliped palm, X_2, on Y_2, data $\bigcirc$. Female data, ♀, not included in analyses.

Morgan collection; log width of cheliped palm, X'_2, on Y', data ●. Female data, ♀, not included in analyses.

Diagnosis

Carapace trapezoidal with two transverse ridges; the anterior margin of the front rather straight except for two notches near centre; supraorbital margins of adults rounded in profile and with several rows of granules; extraorbital spines laterally directed, strongly produced, of moderate breadth at base; anterolateral rises weakly developed, finely granulated. Basal segment of eyestalks exposed. Pterygostomial regions with a stridulating ridge bearing some 77 to 85 transverse striae. Male abdomen seven segmented; first two segments reduced in width; third nearly reaching coxae of last pereiopods and covering most of external spermiduct. Mature cheliped meri with a basal stridulating plectrum and one spinule half way along dorsal margin; palms compressed for most of length; fingers more than half length of palms and with smooth surfaces.

Type material

Holotype, ♂, from Port Curtis, Queensland; No. 50.11, dried collection, British Museum (Natural History). A second specimen from 'Australia' was registered at the British Museum in 1856 (Dr A. L. Rice, pers. comm.).

Material examined

(a) Extant—
    Mature ♂, Q.M. No. W419, Clontarf, Moreton Bay, Queensland.
    Mature ♂, A.M. No. P1147, near Sydney, New South Wales.
    Three juvenile males, A.M. No. P15171 a and b, A.M. No. P15172, trawled at 80 m depth off Cronulla, New South Wales.
    Small ♀, A.M. No. P10090, Sow and Pigs Shoal, Port Jackson, New South Wales.
(b) Fossil and sub-Recent—
    Tentatively referred to *O. macgillivrayi*: fragmentary remains of a cheliped N.M.V. No. P24686, upper shell bed in Jemmys Point Formation in road cutting for Princes Highway on W. side of Bunga Creek, 5·5 km E.N.E. of Lakes Entrance, Gippsland, Victoria. The Jemmys Point Formation is Kalimnan (Pliocene).
    Palm of major (right) cheliped of prob-

ably a male, Q.M. No. F6620, and two specimens of nearly complete carapace, sternum and fragmentary appendages preserved in concretions, Q.M. No. F6624 and Q.M. No. F6625, dredgings at Luggage Point, N. side of mouth of Brisbane River, Moreton Bay, Queensland.

Distribution

Pliocene—? Gippsland Basin, Victoria.
Sub-Recent—Moreton Bay, Queensland.
Extant—The east coast of Australia, from Port Curtis, Queensland, south to off Cronulla, near Sydney, New South Wales. The species is recorded in 'shoal water' at Port Curtis (White, 1852), occurs in the shallow waters of Moreton Bay (Griffin and Campbell, 1969) and has been taken at 80 m depth off Cronulla.

Japan; from Bōsō Province, Sagami Bay, the Kii Straight, Nagasaki, and near the Koshiki Islands. The species is known from a maximum depth of 150 fath. (274 m) at Yodomi on Sagami Bay (Balss, 1922) and from a minimum of 15-13 m at Mitohama, also on Sagami Bay (Sakai, 1965).

Natal; one specimen from the stomach of a fish (*O. pulcher* Barnard, 1950).

Description

The carapace is similar in outline and general form to that of *O. corioensis*. The front is narrow, one eighth of the width of the carapace between the tips of the extraorbital spines; its anterior margin is truncated with two notches separated by a small, acute rostral projection. The front has a border which is prominent on the anterior margin, and markedly dilated adjacent to the deep inner-orbital notches where it bears a shallow groove containing a line of pits.

The supraorbital margins slant rearwards a little and are gently recurved; they have a bluntly rounded profile and bear two rows of coarse granules and several rows of finer granules on the lateral portion. The supraorbital margins of juveniles have an acute profile and one row of coarse granules. Females and juvenile males have a fringe of hairs ventral to the inner two thirds of each supraorbital margin.

The suborbital margins have a rather acute profile, one row of indistinct tubercles, and a sparse fringe of long hairs. They are concave for most of their length, but the inner part is bluntly produced.

The extraorbital spines are laterally directed, strongly produced, and acute, with the base of moderate breadth and the hind margin smoothly curving to the anterolateral regions of the carapace.

Across the anterior third of the carapace is a prominent transverse ridge, the ends of which curve a little towards the posterior and terminate at weakly developed anterolateral rises. Except for the longitudinal mesobranchial crests being lower and more rounded, the carapace of *O. macgillivrayi* is sculptured very similarly to that of *O. corioensis*. The greater part of the surface of the carapace is smooth or minutely granulated; the upper surface of the extraorbital spines, the hepatic regions, the slight anterolateral rises, and the longitudinal mesobranchial crests bear fine, distinct granules.

The slender and elongate eyestalks reach just beyond the tips of the extraorbital spines; both the proximal portion and the cornea are slightly expanded. The first segment is visible in the inner-orbital notch.

The antennules are situated near the centre of the subfrontal region and fold transversely. They are fairly short and have two cylindrical joints before dividing into two short, hair fringed rami. The antennae have three short joints reaching to the corner of the front and then a many-segmented flagellum as long as the whole of one antennule.

The epistome is transversely elongated with the hind margin gently concave on each side of the centre.

Across the anterior part of each pterygostomial region is a curved stridulating ridge bearing some 77 to 85 short transverse striae. The buccal frame is wider than long and slightly wider in front. The surfaces of the pterygostomial and brachiostegal regions are smooth.

The ischium of the third maxilliped is nearly as wide as it is long and has a distinct lateral projection at the base. The merus is subquadrate, three quarters as long as it is wide,

with an obtuse, rounded anterolateral angle. The inner margin of the ischium and the margins of the merus and palp are fringed with hairs. The curved exognath reaches to the first half of the length of the merus, and has a strong, inwardly directed spine near its distal end and a lateral projection at the base.

The sternum is very like that in *O. corioensis* except for a complete, shallow, transverse groove extending between the anterolateral corners of the first large sternite, and somewhat shorter episterna, which reach less closely to the socket for the pereiopod of the next somite.

The abdomen is distinctly seven-jointed; only the ends of the first segment may be exposed from under the carapace. The first and second segments are reduced in width to three quarters the distance between the coxae of the last pereiopods so that parts of the underlying sternite are exposed.

In the male abdomen the third segment covers all but the extreme proximal part of the external spermiduct, which lies in a groove between the sternites corresponding to the fourth and fifth pereiopods. The fourth to sixth segments taper in width; the longest is the sixth. The telson is triangular with a rounded tip.

The female abdomen tapers only slowly from the third segment and thus is much broader than in the male. The telson is of a broad, rounded, triangular shape.

The chelipeds are subequal and elongate. The cheliped ischia have a finely granulated anterior ridge produced to a blunt, distal spine. The meri are elongate and narrow, are slightly arched anteriorly, and have a rounded triangular cross section. They have fine granules on the ventral margin and coarser granules on the anterior and dorsal margins; a blunt spinule is placed mid-way along the length of the dorsal margin. Anterior to a dorsal 'V'-shaped suture, the proximal part of each merus is slightly expanded and bears a short ridge or keel-like plectrum, which opposes the pterygostomial stridulating ridge. The plectrum has a distinct tubercle near its outer end and a sparse fringe of hairs on the ventral aspect. The carpi are smooth and globular with a few pits in the surface and a single bluntly rounded internal spine. The palms are compressed for most of

D

their length and are broadest dorsoventrally with a broad ridge on the inner and outer faces and the upper and lower margins rounded. The upper margin and the ridge on the inner face are distinctly granulated; the lower margin is finely granulated. The fingers are elongate, more than half the length of the palms in mature individuals; they are somewhat compressed laterally and have the surfaces smooth except for a serrated line of teeth on the prehensile margin and a row of distinct tubercles posterior to the tooth row on the distal part of the fixed finger.

Juvenile males have several small spines on the distal part of the anterior margin of each cheliped merus; the carpi have an exterior spine. These spines are not present in slightly larger individuals.

In mature males the extended length of one cheliped is between two and two and a half times the width of the carapace between the tips of the extraorbital spines. The palms have the distal part of the ventral margin compressed; the right palm is a little broader than the left. The right fingers have a large diastema at their symphysis, bluntly rounded proximal teeth, and more acute distal teeth. The fingers of the left hand have only a small gap at the base and the teeth are acute and slightly separated. Curved pincers on the tips of both left and right hand fingers cross when the fingers close.

The cheliped carpi of the female have an external spine. The palms are relatively shorter and slightly broader than in a male of comparable maturity, and have the lower margin compressed. There is no large diastema between the fingers of the right hand. The teeth of the left and right hand fingers are not separated and terminal pincers are not well developed.

The ambulatory legs increase in length in the order 1, 4, 2, 3, with the longest about one and a third times the width of the carapace. The form of the legs differs only slightly from that in *O. corioensis*. The meri of the second, third and fourth pairs of legs are finely granulated on the distal half of the dorsal margin. On the distal part are several larger granules and a short spine, not well developed in males, but prominent in females. The dactyli are compressed dorsoventrally and are curved and narrow with two dorsal grooves containing pits which may or may not hold hairs.

Males have the distal joints of the first and second pairs of legs fringed by hair. The propodi and dactyli of the first pair of legs have two ventral rows of hairs set in pits. A few hairs are present on the third and fourth pairs.

In females the meri and more distal joints of all the legs have fringing hairs.

Heterochely

Normally mature males have the right chela the major.

Dimensions

Measurements are given in Table 3 for the mature male specimen A.M. No. W419 and the female A.M. No. P10090.

Regression analyses

Regression analyses similar to those for *O. corioensis* were made on the five male specimens. The data and analyses are presented in scatter diagrams, Fig. 3A and B, and Table 4. For all the regression analyses 'r' is close to unity, indicating a high positive correlation. The five crabs measured appear to be members of one population.

The slope of the regression lines (Fig. 3A and B) indicates that the growth relationship between the length of the carapace and its width is not quite isometric, and the increase in length of the cheliped palms is positively allometric relative to their width and to the width of the carapace.

Remarks

O. macgillivrayi is the probable descendant of the fossil species *O. corioensis*, from which it differs conspicuously in having the anterior margin of the front doubly notched, not gently sinuous, and the supraorbital margins of the carapace slightly more recurved, rounded in profile rather than acute, and ornamented by several lines of granules, not a single line of spinules. The three basal segments of the abdomen are reduced in width, rather than reaching the full distance between the coxae

of the last pair of legs, and the meri of the chelipeds lack an anterior row of spinules. In *O. macgillivrayi* the basal segment of the eyestalks is exposed; the same segment is apparently covered by the front in *O. corioensis*.

The fragmentary remains of the cheliped from the Pliocene of the Gippsland Basin (N.M.V. No. P24686, Pl. 5, fig. 11) consist of the major part of a left palm and an attached fragment of carpus. While definitely referable to *Ommatocarcinus,* these remains are too fragmentary to be assigned with confidence to any particular species. Nevertheless they markedly resemble the corresponding parts of the chelipeds of males of *O. macgillivrayi,*

FIGURE 3

Regression analyses for selected dimensions of male specimens of *O. macgillivrayi* from eastern Australia. A: Log width of carapace just behind extraorbital spines, X_1, on log carapace length, Y_1, data ●. Female data shown ♀, but not used in analyses.

X_1 on log length of cheliped palm, Y_2, data ○. Female data, ♀, not used in analyses. Coincident data marked with an asterisk.

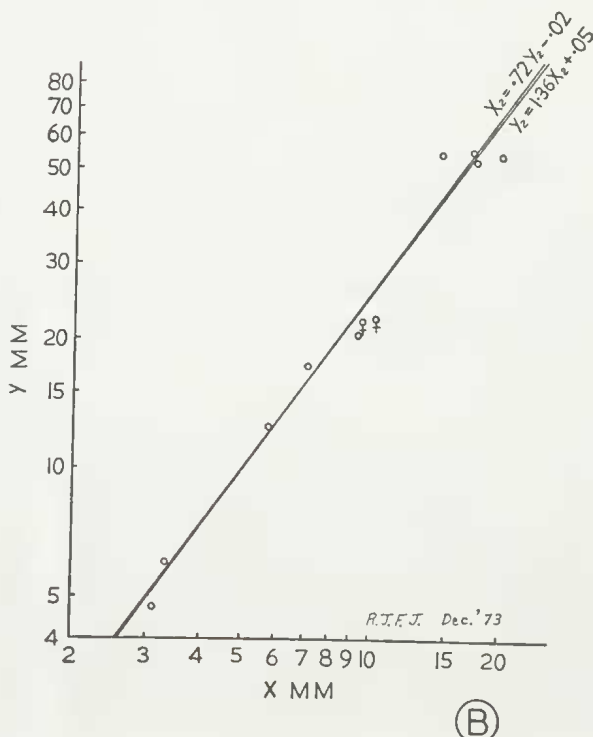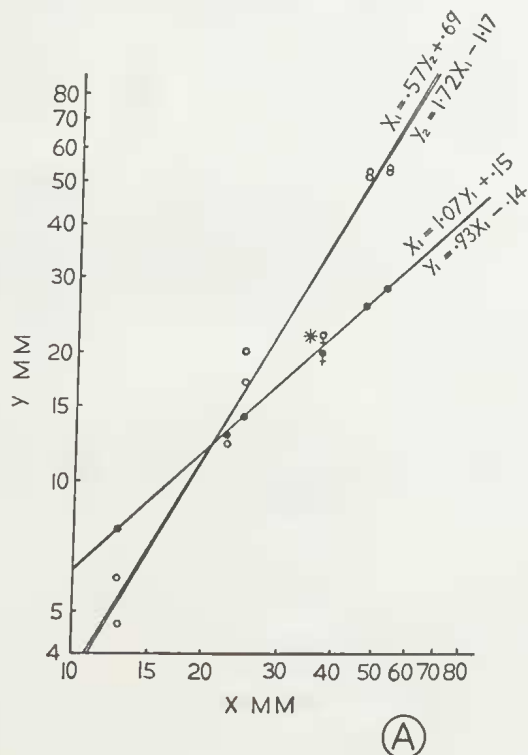B: Log width of cheliped palm, X_2, on Y_2, data ○. Female data, ♀, not used in analyses.

particularly in having a distinct longitudinal groove near the upper margin of the palm, and are thus interpreted as providing a tentative Pliocene record of this species. The sub-Recent remains dredged from Moreton Bay do not differ appreciably from the extant form.

O. macgillivrayi has been recorded from Japan by Balss (1922) and Sakai (1934, 1936, 1939, 1965). Specimens of apparently the same Japanese form were described by Yokoya (1933) as *Ommatocarcinus* sp. From a study of literature Griffin and Campbell (1969) conclude that the Japanese crab does not differ significantly from Australian individuals and I concur with this. The dimensions of the carapace and claws of the rather small specimens illustrated by Yokoya and Sakai plot near the regression lines given here (Fig. 3) for the Australian form.

Takeda and Miyake (1969) point out that *O. pulcher* Barnard 1950, from off Natal, South Africa, cannot be distinguished from *O. macgillivrayi* on the basis of the original description and figures and that they may be synonymous.

TABLE 3

Dimensions of *Ommatocarcinus macgillivrayi* in millimetres

	♂, Q.M. W419	♀, A.M. P10090
Width of carapace between tips of extraorbital spines	66	49
Width of carapace just behind bases of extraorbital spines	52	37
Length of carapace	27	20
Greatest width of front	8·2	6·1
Length of right cheliped	166	68
Length of left cheliped	162	67
Length of right palm	56	23
Length of left palm	56	22
Width of right palm	20	10
Width of left palm	17	9·2
Length of right fixed finger	32	14
Length of left fixed finger	30	13
Lengths of ambulatory legs: first	73	48
second	82	52
third	84	57
fourth	74	49

TABLE 4

Analyses of data indicated on the scatter diagrams comprising Figure 3.
The variables are as explained in the legend of Figure 3.

Bar above numerals in values for coefficient of correlation indicates figure is not significant.

Number of Items of Data	Variables	Coefficient of Correlation	Equations of Regression Lines		Standard Errors for Regression Coefficients		Standard Errors of Estimate	
		r			Syx	Sxy	Sy	Sx
5	X_1, Y_1	$\cdot999$	$Y_1 = \cdot93X_1 - \cdot14$ $X_1 = 1\cdot07Y_1 + \cdot15$		$\cdot0058$	$\cdot0067$	$\cdot0041$	$\cdot0044$
9	X_1, Y_2	$\overline{\cdot999}$	$Y_2 = 1\cdot72X_1 - 1\cdot17$ $X_1 = \cdot57Y_2 + \cdot69$		$\cdot082$	$\cdot027$	$\cdot057$	$\cdot033$
9	X_2, Y_2	$\overline{\cdot998}$	$Y_2 = 1\cdot36X_2 + \cdot05$ $X_2 = \cdot72Y_2 - \cdot02$		$\cdot068$	$\cdot036$	$\cdot060$	$\cdot044$

Ommatocarcinus huttoni Filhol, 1885

Fig. 9, Pl. 7, figs. 3a-c, 4a-b.

Ommatocarcinus huttoni Filhol, 1885: 384-385, pl. 43, figs. 1, 2, 5.
Ommatocarcinus macgillivrayi White. Miers, 1886: 247-248.
Neommatocarcinus huttoni (Filhol). Takeda and Miyake, 1969: 175-179 (detailed synonomy), figs. 5 and 6, pl. 2, fig. A.

Diagnosis

Carapace trapezoidal, fairly broad, without transverse ridges, anterior margin of front gently concave except for a small, acute, rostral projection, supraorbital margins subangular in profile with a line of distinct granules, extra-orbital spines laterally directed, acute, and stout, anterior ridge of pterygostomial regions not adapted for stridulating. Male abdomen reduced in width; third segment not covering external spermiduct; segments 3 to 5 fused.

Adult cheliped meri lacking distinct spinules and without a stridulating plectrum. Mature male cheliped palms with proximal portion narrow and rounded; fingers about one-third length of palms and with surfaces distinctly granulated.

Type material

According to Filhol (1885), his single specimen (holotype) from near Otago, New Zealand, was lodged in the Muséum National d'Histoire Naturelle, Paris.
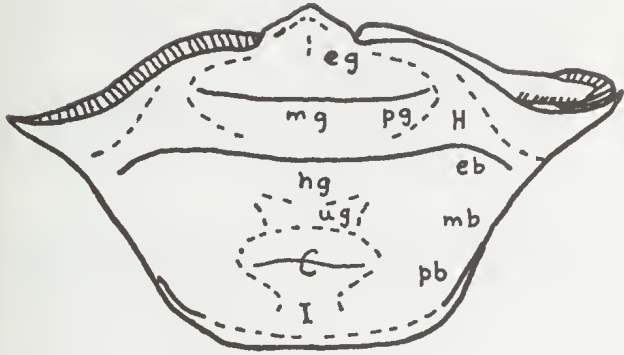
FIGURE 4
Other described species of Ommatocarcinus:
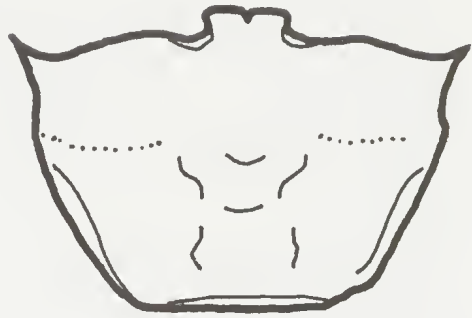A: *Ommatocarcinus zariquieyi* Vía; carapace, x 3. (After Vía, 1959).
B: *O. arenicola* Glaessner; carapace, x 1½. (After Glaessner, 1960).
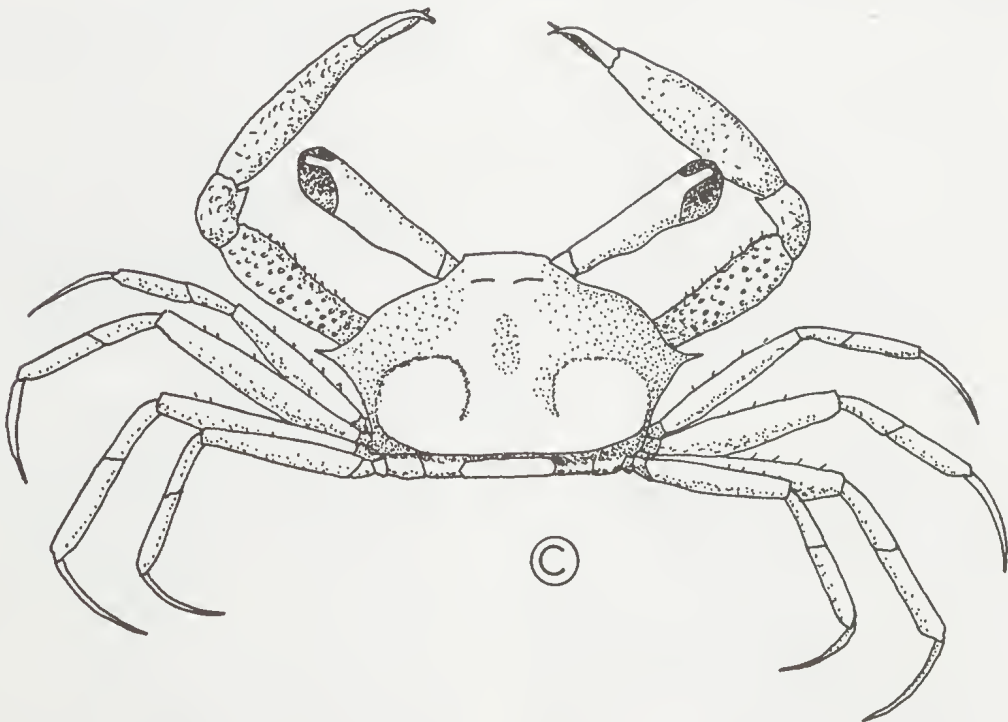C: *O. orientalis* Tesch; dorsal view, x 10. (After Tesch, 1918).
D: *O. fibriophthalmus* Yokoya; dorsal view, x 3. (After Yokoya, 1933).
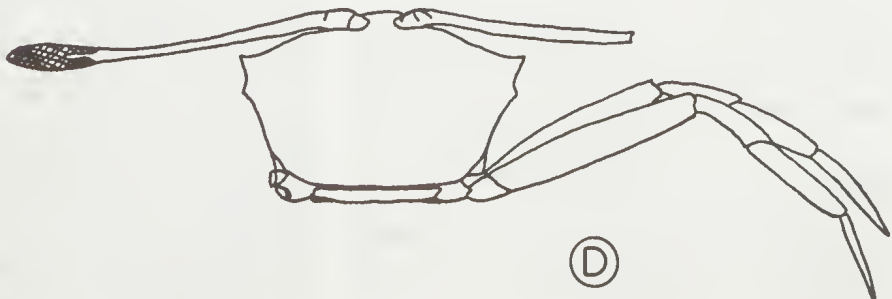
eg, mg, Pg, H, eb, hg, ug, C, I, mb, pb

Material examined

Mature ♂, from 20-28 fath (37-51 m) between 8 and 10 km off Greymouth Bar, west coast of the South Island of New Zealand: D.M. Cr 1765.

Mature ♀, trawled from Cook Strait, New Zealand: D.M. Cr 1171.

Distribution

New Zealand and the Chatham Islands. For details see Takeda and Miyake, 1969.

Remarks

Takeda and Miyake (1969) have described this species in detail and compared and contrasted it with *O. macgillivrayi*.

Other members of the genus

In addition to the *Ommatocarcinus* species described or diagnosed above, the following other forms are known:

O. zariquieyi Vía, 1959
Figs. 4a and 9

Eocene, Middle Lutetian; Cataluna, Spain.

O. arenicola Glaessner, 1960
Figs. 4b and 9

Otaian to Waiauan, early Lower to Middle Miocene; Waipara River, South Island of New Zealand.

O. sp. Glaessner, 1960

Awamoan, late Lower Miocene; Oamaru, South Island of New Zealand.

O. orientalis Tesch, 1918
Figs. 4c and 9

Near the Kei Islands, at 90 m depth.

O. fibriophthalmus Yokoya, 1933
Figs. 4d and 9

Between Tsushima Island and Gotō Island, Japan, at 146 m.

Recent reviews of these species are given by Takeda and Miyake (1969) and Vía (1970).

Preservation and stratigraphic distribution of O. corioensis

Preservation

The materials of *O. corioensis* studied are preserved in one of three ways:

(a) natural skeletal material *in situ* in sediments;

(b) skeletal material enclosed within phosphatic concretions which formed *in situ* in sediments;

(c) skeletal material enclosed within water-worn phosphatic nodules concentrated at the base of certain beds.

The remains preserved *in situ* in sediments almost always have the appendages attached in place and are positioned in a life-like attitude. The inferred significance of this remarkably complete preservation is discussed in a following section on palaeoecology (pp. 52-54). Traces of coloration are sometimes evident in this material.

Examples of the crab within concretions are known from the Miocene at Port Campbell and the Geelong area, and the Pliocene near Hamilton, Victoria. The concretions have a dense, brown or dark coloured centre in which the crabs, other shelly fossils and sand grains are cemented; there is a gradation in the degree of cementation to the enclosing unaltered sediments. The crab remains appear to have served as a nucleus for the diagenetic concentration of phosphatic material which replaced the carbonate minerals in the sediment about the fossil.

Remains of the crab within water-rounded phosphatic nodules are well known from the Geelong area, where localized concentrations of phosphatic nodules occur frequently at the base of the Moorabool Viaduct Sands (Coulson, 1932; Kebble, 1932; Bowler, 1963). About 20 per cent of the nodules in these concentrations enclose fossils of *O. corioensis* or remains of the thalassinid *Ctenocheles* Kishinouye. The preservation of the crabs in the water-rounded nodules is identical to that in the concretions mentioned above. Bowler (1963) considered that the nodules, both with and without crabs, are remanié and represent water-abraded concretions eroded from Miocene and possibly older sediments. This view is accepted here in contradistinction to the suggestion of Coulson (1932) and Kebble (1932) that the crab-containing nodules formed in a mud bed deposited in a transgression postdating the major Miocene phase of deposition, and pre-Kalimnan. Similar

remanié occurrences of the crab in phosphatic nodules occur widely in the Pliocene of southern Victoria and nodules containing *O. corioensis,* and apparently formed in the same way, have recently been dredged from the upper part of the continental slope off New South Wales (von der Borch, 1970; here p. 52). In this paper the terms 'concretion' and 'nodule' are uniformly applied in the sense outlined above.

Stratigraphic distribution

O. corioensis occurs widely in the marine Tertiary sediments of south eastern Australia (Fig. 5). The stratigraphic distribution is outlined in Figure 6 in which the separate occurrences are indicated within the framework of the recognized tectonic-sedimentary basins. The occurrences are as follows:

Murray Basin

Two isolated fingers are from the lower member of Morgan Limestone, section C, Hundred of Cadell, 6 km south of Morgan, South Australia. Early part of *Praeorbulina glomerosa curva* zone of Ludbrook and Lindsay (1969), late Lower Miocene.

Some 25 or so remains are from the top part of the upper member of Morgan Limestone, section C, Hundred of Cadell, near Morgan. Later part of *Praeorbulina glomerosa curva* zone of Ludbrook and Lindsay (1969), latest Lower Miocene.

Four specimens are from Morgan Limestone, near Waikerie, South Australia. Late Lower to earliest Middle Miocene.

Otway Basin

Over 100 remains are from Port Campbell Limestone, sea cliffs in the vicinity of Port Campbell, Victoria; specimens occur in argillaceous limestone above Rutledge's Creek Member and purer limestone near the cliff tops. Localities include: top of London Bridge, cliff top at Point Hesse, Two Mile Beach (Hall, 1905), Gravel Point, notch on E. side of Amphitheatre, mouth of Sherbrook River, cliffs at Beacon Steps (Baker, 1945) and cliffs opposite Sentinel Rock (Baker, op. cit.). *Globorotalia lenguaensis—Globorotalia mayeri* Zonule to *Globorotalia miotumida Zonule* of

Taylor (*in* Singleton, 1968; *in* McGowran et al., 1971); mid Middle Miocene to ?Upper Miocene.

One specimen is from Port Campbell Limestone, Curdies River Lime Works, Curdie, Victoria. ?Middle to ?Upper Miocene.

One specimen is from Port Campbell Limestone, 3 km W. of Timboon, Victoria. ?Middle to ?Upper Miocene.

A number of fragmentary remains are in remanié phosphatic nodules at base of the Grange Burn Formation, Grange Burn, 8 km W. of Hamilton, Victoria. The Grange Burn Formation is Kalimnan or Pliocene (Spencer-Jones, 1971; Taylor, 1971, p. 236). The nodules are probably derived from underlying Miocene sediments.

Two specimens are in phosphatic concretions, Grange Burn Formation, 1 m above (normal?) creek level, Forsyths Bank, Grange Burn. Kalimnan, Pliocene.

One specimen comes from the thin limestone bed 10 m below the top of Fyansford Clay, Amphitheatre on Leigh River, 6 km N. of Shelford, Victoria. *Globigerinoides sicanus* zone of Ludbrook and Lindsay (1969) (data Dr Mary Wade, pers. comm.), late Lower Miocene.

Several remains are in remanié phosphatic nodules, from the base of Moorabool Viaduct Sands, Amphitheatre on Leigh River near Shelford. The Moorabool Viaduct Sands are Upper Miocene (Aziz-ur-Rahman and McDougall, 1972). The nodules are probably derived from the underlying Fyansford Clay.

Two specimens are in phosphatic concretions, from a thin sandy limestone interbed in Fyansford Clay, 0·5 km N.E. of the junction of Bruces Creek and Barwon River, near Murgheboluc, Victoria. Start of *Orbulina universa* zone of Ludbrook and Lindsay (1969) (data Dr Mary Wade, pers. comm.); early Middle Miocene.

Two specimens come from the Fyansford Clay, left bank of Barwon River, section 2B, Parish of Murgheboluc, Victoria. Start of *Orbulina universa* zone of Ludbrook and Lindsay (1969), early Middle Miocene.

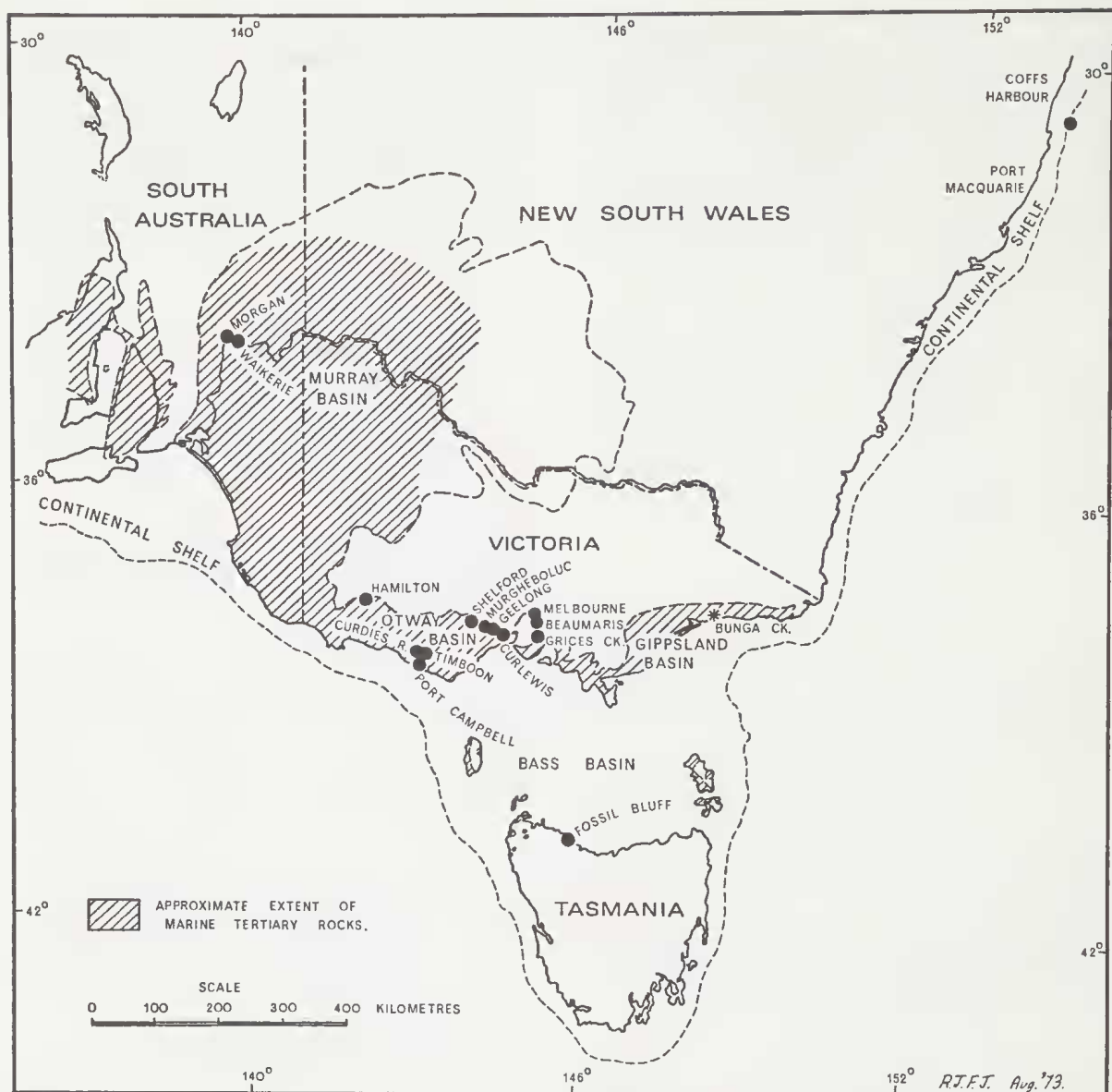Specimens are reported to occur in a thin

FIGURE 5

Locality map showing occurrences of fossil remains of *Ommatocarcinus* in southeastern Australia. ●, *Ommatocarcinus corioensis* (Cresswell). *, fragmentary remains tentatively identified as *Ommatocarcinus macgillivrayi* White.

limestone bed with *Hinnites corioensis* McCoy, Fyansford Clay, North Shore, Geelong, Victoria (Singleton, 1968). Bairnsdalian (Bowler, 1963), Middle Miocene.

Numerous remains are in remanié phosphatic nodules from the base of Moorabool Viaduct Sands, Geelong area, Victoria. Localities include Murghcboluc, Batesford, Fyansford, Cowies Creek, North Shore and Western Beach at Geelong, the vicinity of Fenwick, and the sea coast near Curlewis (location of lectotype). The nodules are probably derived from underlying Miocene sediments.

Fragmentary remains not enclosed in nodules are reported by Kebble (1932) as occurring in phosphatic nodule bed (base of Moorabool Viaduct Sands) in the Geelong area. They are possibly from *in situ* in Moorabool Viaduct
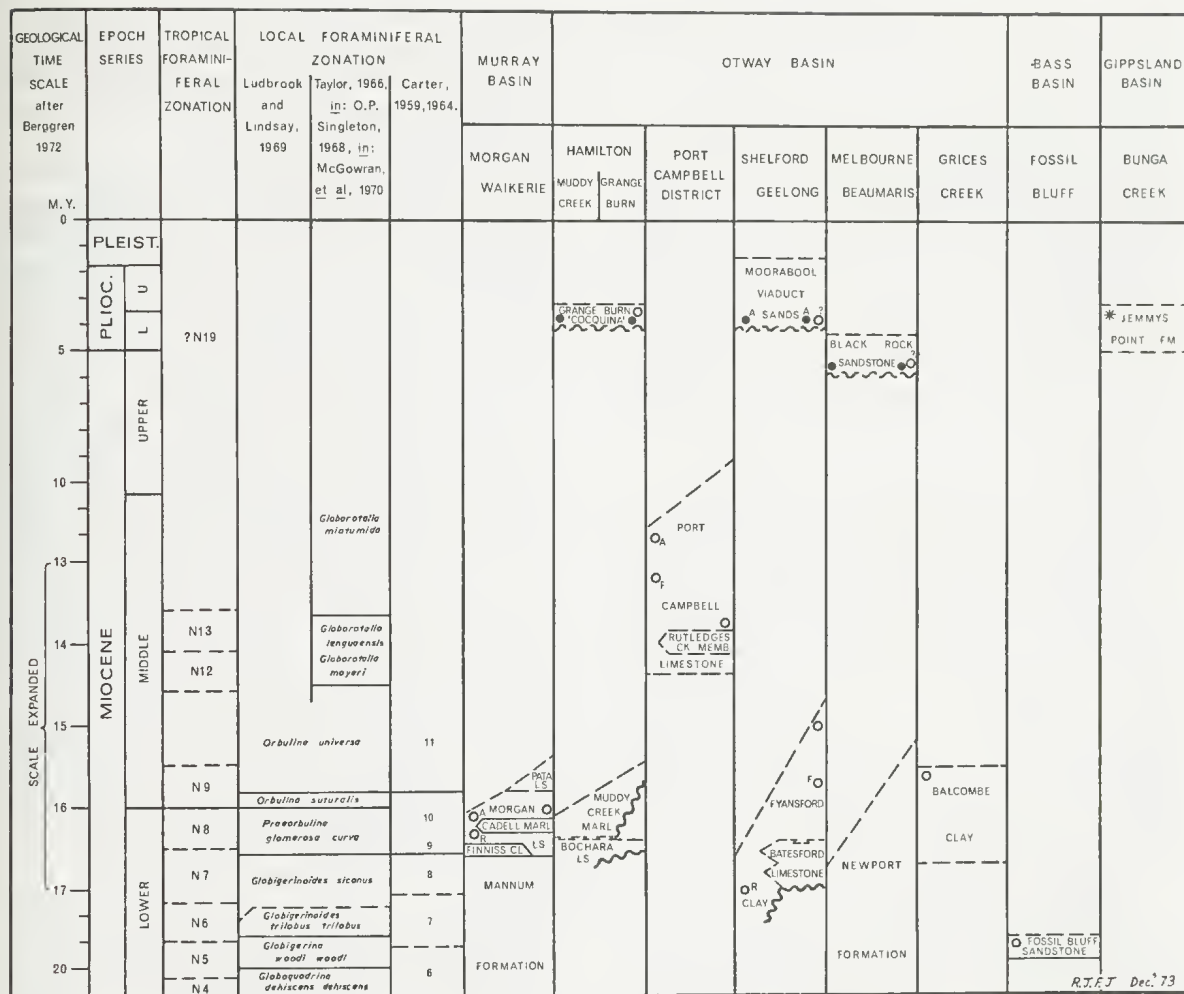
FIGURE 6

Stratigraphic distribution of *Ommatocarcinus* in southeastern Australia:
○: Occurrences of *O. corioensis in situ* (specimens from the Upper Miocene of the Geelong area and Beaumaris may possibly be remanié). ●: Occurrences of *O. corioensis* in remanié phosphatic nodules. *: Single fragmentary claw referred tentatively to *O. macgillivrayi*. A, specimens abundant. F, specimens frequent. R, specimens rare. Geological time scale after Berggren (1972).

Sands or derived from soft facies of underlying Miocene sediments.

Remains occur in remanié phosphatic nodules from the base of Black Rock Sandstone, Melbourne area, Victoria. Localities are a railway cutting at South Yarra, and the sea coast at Beaumaris. The Black Rock Sandstone is Cheltenhamian, late Miocene to ?early Pliocene.

Seven more or less fragmentary remains of uncertain stratigraphic level are known from the sea coast at Beaumaris. They are possibly from *in situ* in Black Rock Sandstone and Cheltenhamian, or remanié, derived from underlying Newport Formation of Lower to Middle Miocene age.

A pair of chelae came from Balcombe Clay, the downstream section of Grices Creek, 5 km N.N.E. of Mornington, Victoria. Faunal Unit 11 of Carter (1959, 1964), Bairnsdalian (Gostin, 1966), Middle Miocene.

Bass Basin

One specimen has been taken from Fossil Bluff Sandstone, Fossil Bluff, near Wynyard, northwest Tasmania. Faunal Unit 6 of Carter

(1959, 1964) according to Quilty (1972), Lower Miocene.

Continental slope off New South Wales

Two fragmentary remains in nodules are from the upper part of the continental slope off New South Wales (materials kindly donated by Professor C. C. von der Borch). One nodule was from 210 m depth at 30°41'S, 153°18'E off Coffs Harbour; the second from a depth of 247 to 274 m in the region of Coffs Harbour or Port Macquarie. The nodules are probably reworked concretions eroded from sediments of Miocene age (von der Borch, 1970).

Conclusions

The stratigraphic range of *O. corioensis* is from within the Lower Miocene to the Pliocene. The numbers of specimens taken *in situ* in different stratigraphic intervals suggests that the species was rare during most of the Lower Miocene, numerous or even abundant at different times in the late Lower and early Middle Miocene and mid Middle to ?Upper Miocene, and relatively uncommon in the late Upper Miocene and Pliocene. None of the possible Upper Miocene occurrences have been verified with certainty.

O. corioensis has not been recorded from the St. Vincent Basin of South Australia. The better known exposures of mid-Tertiary sediments in this basin predate the late Lower Miocene increase in abundance of the species.

Palaeoecology of O. **corioensis**

Mode of occurrence

Remains of *O. corioensis* found *in situ* are usually preserved in a life-like attitude with the dorsal aspect uppermost (Fig. 7A, B, Pl. 4, figs. 5a-d, Pl. 5, figs. 1a, 2a, 6 and 9). The fossils may either be remains of dead animals or moults, since the pleural sutures are invariably fractured. If they are moults the carapace has fallen back into place in the manner described by Schäfer (1951). It is considered more likely that most are remains of dead animals and that the sutures were weakened by post-mortem decalcification and broken due to compaction of the enclosing sediment. Almost all specimens are slightly crushed, some greatly so. The atti-

tude in which the crabs are preserved indicates that their appendages have been supported by the sediment enclosing them (Fig. 7B), and suggests that the animals were already buried at the time of death.

Hall (1905) suggested that the conditions of preservation of remains of *O. corioensis* occurring in the cliffs of the Port Campbell area indicated that the crabs were 'entombed in their burrows'. The writer has found specimens associated with fossil burrows weathering out of the flat bedding-plane erosion surfaces which form in the Port Campbell Limestone on the tops of these cliffs (Pl. 8, figs. 2 and 3). The burrows are usually sub-cylindrical structures 3-6 cm wide and lying more or less in the plane of the bedding. Frequently they form branching complexes with individual forks at intervals of 5 cm to 1 m apart (Fig. 7C and D, Pl. 8, figs. 1 and 5). Often the burrows are deeper than wide and have a layered infilling, the layers curving obliquely upwards towards the roof of the structure (Pl. 8, fig. 4); this layering may have resulted from the crab plastering material onto the bottom of the burrow. Other crabs are associated with more or less irregular structures which may represent an infilled funnel leading down to a burrow.

The burrows are clearly dwelling structures (*Wohnbauten* of Seilacher, 1953) which the animal maintained and occupied for a significant length of time, probably for protection. The burrows strikingly resemble those which Rice and Chapman (1971) describe for the extant, European *Goneplax rhomboides* (Linné) a crab closely related to *Ommatocarcinus*. The males of *Goneplax* have the chelipeds similarly

FIGURE 7

A-B: *Ommatocarcinus corioensis* (Cresswell); A, reconstruction of ♂ specimen N.M.V. P24721 in dorsal view, showing its life-like attitude as preserved in the sediment (cf. Pl. 5, fig. 1), x 11/12; B. partial reconstruction of crab in lateral view showing how its appendages were evidently supported by a level of sediment no lower than the line X, Y at the time of preservation, x 1¼.

C-D: Burrow complexes attributed to *O. corioensis* and occurring in the Port Campbell Limestone at the mouth of the Sherbrook River near Port Campbell; e, assumed position of entrance funnel; complex illustrated in D also shown in Pl. 8, fig. 5.

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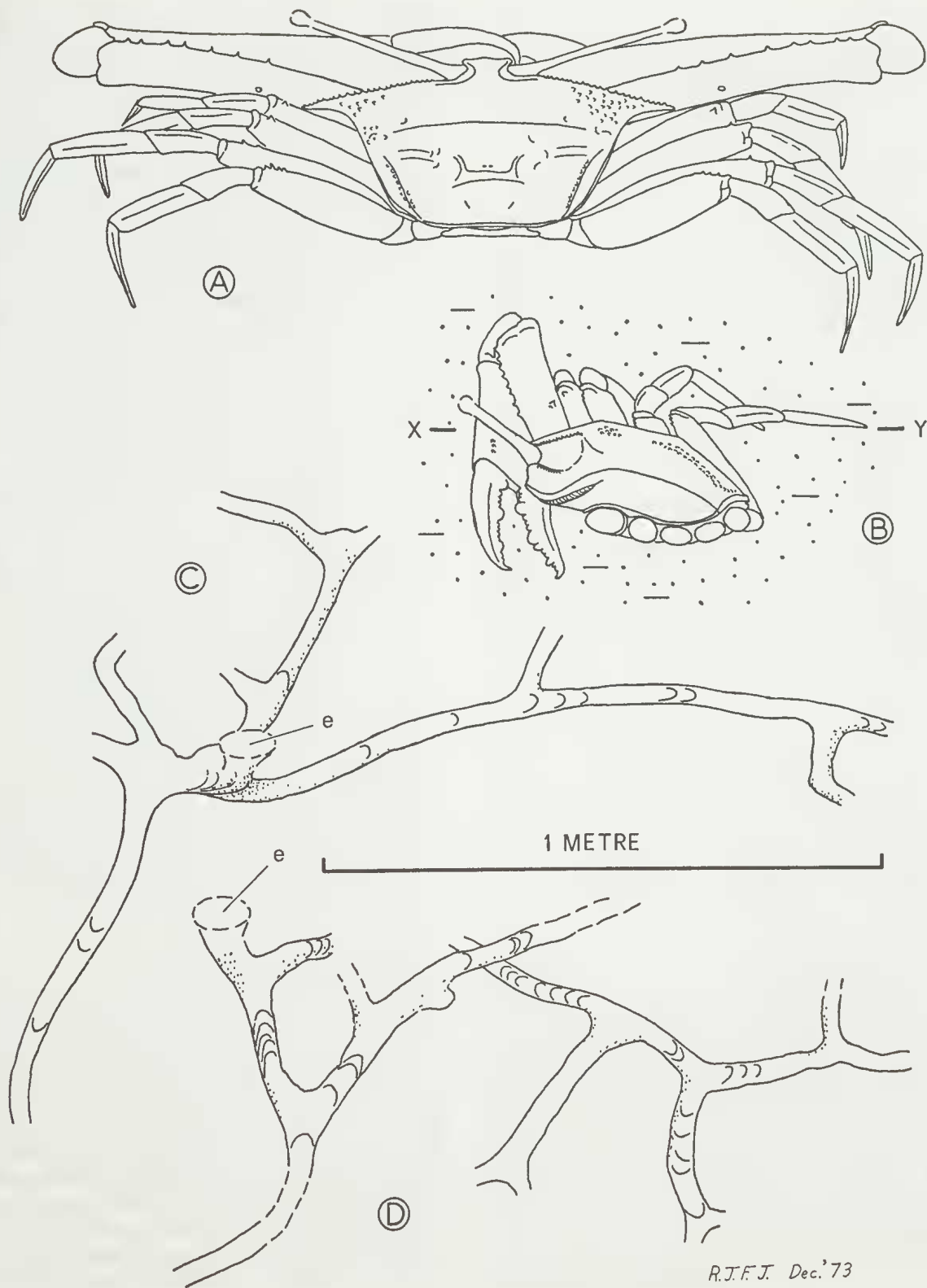
elongated as in *Ommatocarcinus* and Rice and Chapman document the important function of the chelipeds in either pushing mud away from the crab or carrying mud during burrowing. It seems highly probable that the chelipeds of *Ommatocarcinus* are adapted to perform the same function. The elongate eyestalks of *Goneplax* fold laterally into trough-like orbits as in *Ommatocarcinus,* thus enabling the crab to move sideways along narrow passageways.

Very numerous remains of *O. corioensis* in the Port Campbell cliffs and at other localities do not show any relationship to obvious burrow structures. Possibly these animals died after digging down into, and burying themselves in loose sediment. Hence *O. corioensis* may have constructed semi-permanent burrows as well as being able to rapidly bury itself for protection when distant from a dwelling burrow.

Keble (1932) noted that collections of *O. corioensis* from *in situ* tend to have a preponderance of smaller individuals. This has been verified for the Port Campbell Limestone where individuals with the carapace only 9 mm wide may be found. The abundance of smaller individuals is suggestive of an approximation to a life-assemblage or biocoenose (see Boucot, 1953).

In all the collections at my disposal there is a notable inequality in the numbers of each sex; males are about ten times more numerous. This inequality may partly reflect preferential preservation of long clawed specimens in phosphatic concretions and nodules, but is not readily explicable for unphosphatized, non-remanié remains occurring *in situ.*

Life environments

O. corioensis is a relatively common fossil in the top 3 m interval of the upper member of the Morgan Limestone, 6 km south of Morgan. A count of 120 shells of the bivalve *Spondylus pseudoradula* McCoy occurring in a bed within this interval gave a ratio of about 1:5 for the number of articulated valves against disarticulated valves. Hence these beds appear to have been deposited in a relatively low-energy environment, but in water certainly shallower than wave base. The fauna of the interval suggests a shallow environment and

includes the brachiopod *Magellania macleani* (Tate), separated valves of *Ostrea* Linné, cirripedes (attached to shells), remains of the thalassinid decapods *Callianassa* Leach and *Ctenocheles,* the large benthonic foraminifera *Marginopora* Quoy and Gaimard, and small coralline algae. Some of the latter are grouped together in life orientation. In modern seas *Marginopora* is most common in very shallow water down to 27 m in depth (Adams, 1965). Coralline algae are mainly found at tide level to 30 m deep (Johnson, 1961). Hence at this locality *O. corioensis* probably lived in moderately active waters less than 30 m deep.

Bowler (1963) analysed the environment of deposition of the Fyansford Clay at North Shore, Geelong, another locality for *O. corioensis.* On the basis of the lithology, the sand clay ratio and the mineralogy of the sediments, he suggests that deposition occurred in 'very shallow' water which was alkaline and had a positive Eh.

The most abundant occurrence of *O. corioensis* known is in the Port Campbell Limestone, which Glenie (1971) characterizes as a transgressive, neritic, marine unit. Singleton (1968) suggests that this limestone was deposited in a quiet off-shore environment, but not pelagic, and considers that the relatively fine grained, bioclastic, lime sands composing it were washed in from shallow water. Thus the depth range of *O. corioensis* was probably not dissimilar to that of the living *O. macgillivrayi,* which is known from 'shoal water' to 80 m in Australian waters and down to 274 m off Japan.

Associated sediment type

All specimens, including those in phosphatic nodules, appear to have been originally fossilized in limcy sediments. Of the specimens collected *in situ,* 76 per cent are in fine grained bioclastic limestones which have a high proportion of foraminiferal fragments, a little glauconite, and some silt. Thirteen per cent are enclosed by silty calcarenite or marl with other shelly fossils. Seven per cent have a matrix of calcareous siltstone; and four per cent are in calcarenites with some quartz sand. The two largest percentages given are disproportionately

high due to extensive collecting from large outcrops.

Selected examples of the matrix of different specimens had a silt-clay fraction ranging from 9 to 53 per cent of the rock by weight. Only a few grains of quartz sand were present. One calcarenite matrix contained five per cent by weight of fine to medium grained angular quartz sand and a little silt.

The general association of *O. corioensis* with relatively fine grained sediments almost certainly reflects its burrowing habits. A sediment fine enough for ready excavation but not so fine as to smother the crab or collapse readily seems to have been preferred. The apparent close association with limey sediments may be an artefact of the nature of the materials being chiefly deposited; quartz rich sands of similar age are rare in southern Australia.

Isotopic temperatures and relative abundance

Dorman (1966) presents numerous relatively recent results of oxygen isotope temperature measurements made on shelly fossils, mainly bivalves, collected from the Tertiary rocks of southern Victoria. A comparison between some of the better dated items of this data and the numbers of *O. corioensis* found in different stratigraphic intervals is shown in Figure 8. The crab is a rather rare species during most of the Lower Miocene, but becomes abundant during the latest Lower Miocene and earliest Middle Miocene. It is again abundant during the later part of the Middle Miocene (and possibly early Upper Miocene). There is little or no evidence to relate these times of abundance with the relatively high isotopic temperatures of 23-25°C. recorded in the late Lower and Middle Miocene. Rather, the crabs seem to have been common during cooler intervals with isotopic temperatures of the order of 14-17°C. Tropical crab genera, *Calappilia* A. Milne Edwards and a tropical section of *Nucia* Leach, appear in the southern Australian Tertiary during the high temperature interval of the late Lower Miocene (Jenkins, 1972), and ingressions of the warm water foraminifera *Lepidicyclina* Gümbel, *Cycloclypeus* Carpenter and *Marginopora* at this time (Carter, 1964; Lindsay, 1969, 1970; Lindsay and Giles, 1973)

are clearly related to the same event (Fig. 8). A distinctly later ingression of the warm water, foraminiferal genus *Flosculinella* Schubert and Richarz is linked to the appearance of *Orbulina suturalis* Bronnimann in the Adelaide Plains Sub-Basin of the Port Vincent Basin (Lindsay, 1969). As later members of the *Orbulina* bioseries occur only rarely in the Adelaide Plains Sub-Basin (Lindsay, 1969, p. 38), this dating of the *Flosculinella* ingression cannot be regarded as sharply fixed. It thus seems plausible that the ingression of this genus is related to the high-temperature event during the *Orbulina universa* Zone.

The possible *in situ* occurrences of *O. corioensis* in the latest Miocene (Beaumaris and Geelong district) and its better documented occurrences in the Pliocene of Grange Burn, Hamilton, seemingly relate to isotopic temperatures of 13-18°C. The living *O. macgillivrayi* is known along the eastern Australian coast between 24°S and 34°S, where sea-water temperatures between 0 and 100 m depth range from about 14-17°C. to above 27°C.

As well as to the direct influence of climate, the abundance of *O. corioensis* is probably also linked to its burrowing habits and sediment facies. For most of the Lower Miocene the marine sediments of the Murray Basin and western parts of the Otway Basin were chiefly rather coarse grained bioclastic limestones, while similar limestones and fossiliferous clays predominated in the central and eastern parts of the Otway Basin. Deposition of silty limestones, calcareous silts and silty marls became widespread in the late Lower Miocene (e.g. the Morgan Limestone, Fyansford Clay and Balcombe Clay) and it is in these sediments that *O. corioensis* first becomes numerous. This phase of sedimentation was evidently a secondary result of climate; the influx of silt from erosion of a mature extra-basinal topography which underwent deep chemical weathering during the preceding time of near-tropical climate, coupled with the continuing high productivity of shelly organisms in the warm, shallow seas. The Port Campbell Limestone was a localized, relatively fine-grained off-shore facies which was obviously highly suited to the life habits of the crab.

FIGURE 8

Comparison between the numbers of specimens of *Ommatocarcinus corioensis* found *in situ* at different localities representing various ages (occurrences numbered 1-15) and oxygen isotope temperature data for the region of southern Victoria. The correlation of Lower and Middle Miocene data is based largely on planktonic foraminifera; correlations for later times based largely on mollusca. The isotope temperature measurements are selected from data presented by Dorman (1966); his numbering of each item is indicated. The fossil crab localities are as follows: 1, Fossil Bluff; 2, Amphitheatre, Shelford; 3, lower member of Morgan Limestone at type section near Morgan; 4, section 2B Murgheboluc; 5, upper member of Morgan Limestone at type section near Morgan; 6, Waikerie; 7, Murgheboluc (specimens probably more numerous than data suggests); 8, Grices Creek; 9, North Shore, Geelong; 10, Port Campbell Limestone, apparently not far above Rutledges Creek Member, Amphitheatre near Port Campbell; 11, same locality as 10, higher in cliff; 12, Port Campbell Limestone, cliff tops in Port Campbell area; 13, Beaumaris (specimens possibly remanié); 14, Geelong area (specimens possibly remanié); 15, Grange Burn, near Hamilton.

Distribution and evolution of Ommatocarcinus

The known range of the genus is from the Middle Eocene to the present. *O. zariquieyi,* the oldest known species, occurs in the Middle Eocene of north eastern Spain. Presumably the genus migrated along the Tethys to the Indo-Pacific region, where *O. corioensis* and *O. arenicola* are the earliest known forms. *O. corioensis* is first recorded from early Miocene rocks in Tasmania; *O. arenicola* occurs in the Lower Miocene of the South Island of New Zealand.

With the exception of *O. orientalis,* the modern representatives of the genus are restricted to the sub-tropical and temperate climatic zones. The fossil species are found in latitudes similar to those inhabited by the recent forms.

As is suggested earlier in this paper the
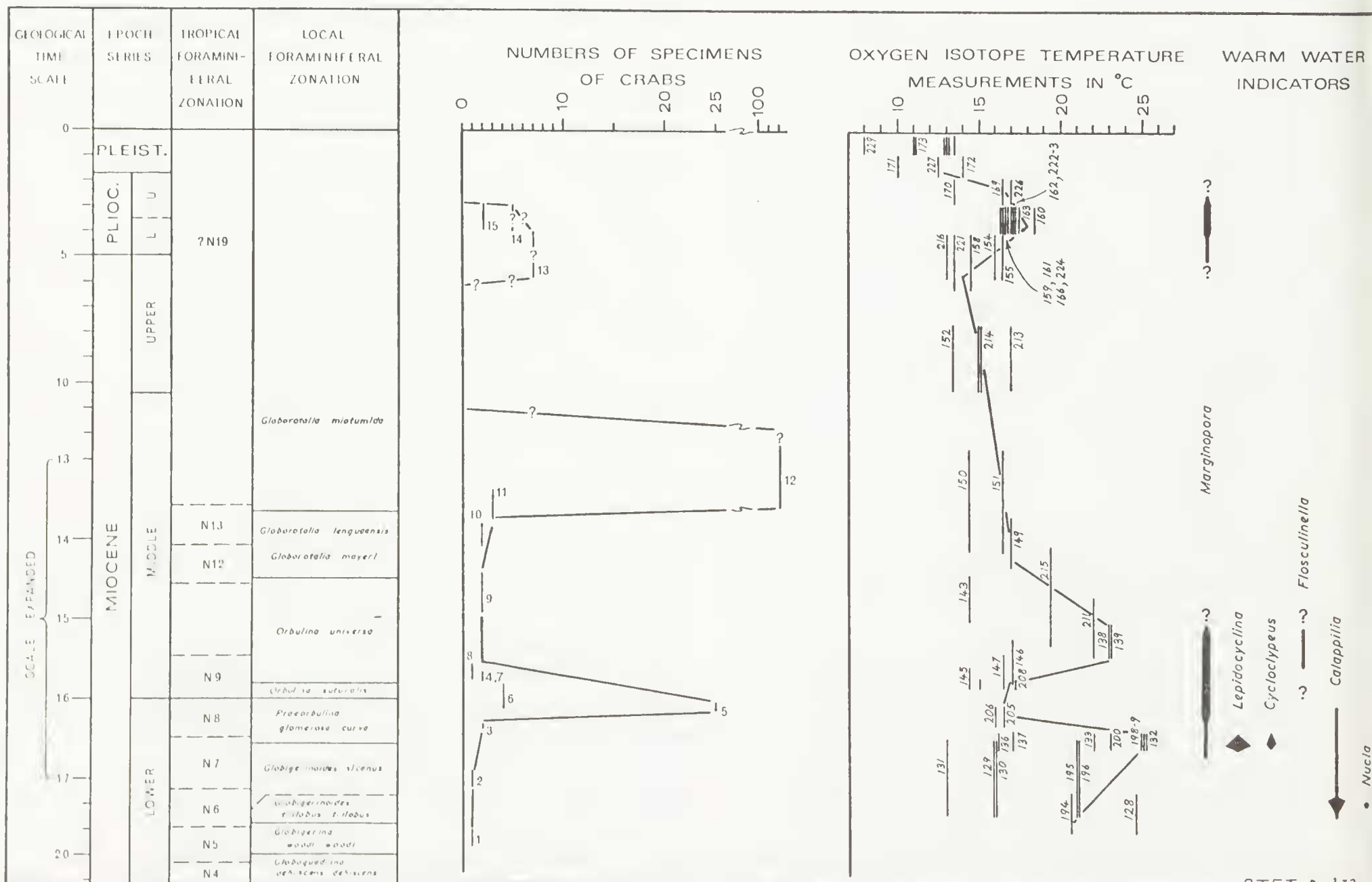
occurrence of *O. corioensis* in southeastern Australia probably reflects water temperatures somewhat warmer than at present. It extended 4° to 7° further south than the known range of the living *O. macgillivrayi,* and is most abundant during the latest Lower and early Middle Miocene, and late Middle Miocene, when oxygen isotope temperature measurements on other shelly fossils give values of 14-17°C. Its abundance is also linked to phases of deposition of soft sediments which enabled it to pursue its burrowing habits.

Water temperature apparently influences the modern distribution of *O. macgillivrayi* near Japan (Yokoya, 1933). Where the warm Kuroshio Current touches on the east coast of Japan the crab is found as far north as the Bōsō Peninsula (latitude approximately 35°N). West of Japan the warm northward current meets the cooler water of the Japan Sea and *O. macgillivrayi* is known only as far north as Nagasaki (latitude 32°48′N). Transport of pelagic larvae by an eastward current probably enabled *O. huttoni* to reach the Chatham Islands from New Zealand (Dell, 1968). *Ommatocarcinus* is not recorded from the Americas. The Atlantic and Pacific appear to have formed eastern and western barriers respectively.

Members of *Ommatocarcinus* strikingly resemble species of *Goneplax,* not only in the general features of their morphology such as the shape of the carapace and the elongate eyestalks and chelipeds, but also apparently in behaviour, notably the habit of burrowing. Glaessner (1960) indicated the close similarity between the outline of the carapace of *O. arenicola* and the living *Goneplax rhomboides,* the type species of *Goneplax.* The resemblance is at least as great between *O. arenicola* and *Goneplax gulderi* Brachmayer from the Tortonian (Upper Miocene) of Austria. *Goneplax* is not recorded earlier than the Middle Miocene (*Goneplax* cf. *sacci* Crema, Glaessner from the Helvetian of Austria). Thus it is suggested that *Goneplax* evolved from *Ommatocarcinus* (Fig. 9).

In the evolutionary lineages within *Ommatocarcinus,* tentatively indicated in the same figure, several trends are apparent. The front is rostrate in the oldest known species, but anteriorly truncated and with deep innerorbital notches in all later forms. The change in form of the anterior margin of the front appears to be an adaptation to allow greater freedom of movement of the antennules; the anterior margin is gently concave above the antennules in *O. corioensis, O. huttoni* and *O. orientalis,* while in *O. macgillivrayi* distinct antennular notches are present. The innerorbital notches narrow the front and probably facilitate erection of the eyestalks. It is notable that the basal segment of the eyestalks is concealed below the front in *O. corioensis* (and apparently in *O. zariquieyi*), but is exposed in all the extant species. In *Goneplax* the evolution of the front has evidently been more conservative and the inner-orbital notches are relatively shallow.

Another tendency in *Ommatocarcinus* is for reduction of the male abdomen. In *O. huttoni, O. orientalis* and *O. macgillivrayi* the basal segments of the abdomen are variously reduced in width. The third, fourth and fifth segments are fused in *O. zariquieyi* and *O. huttoni.*
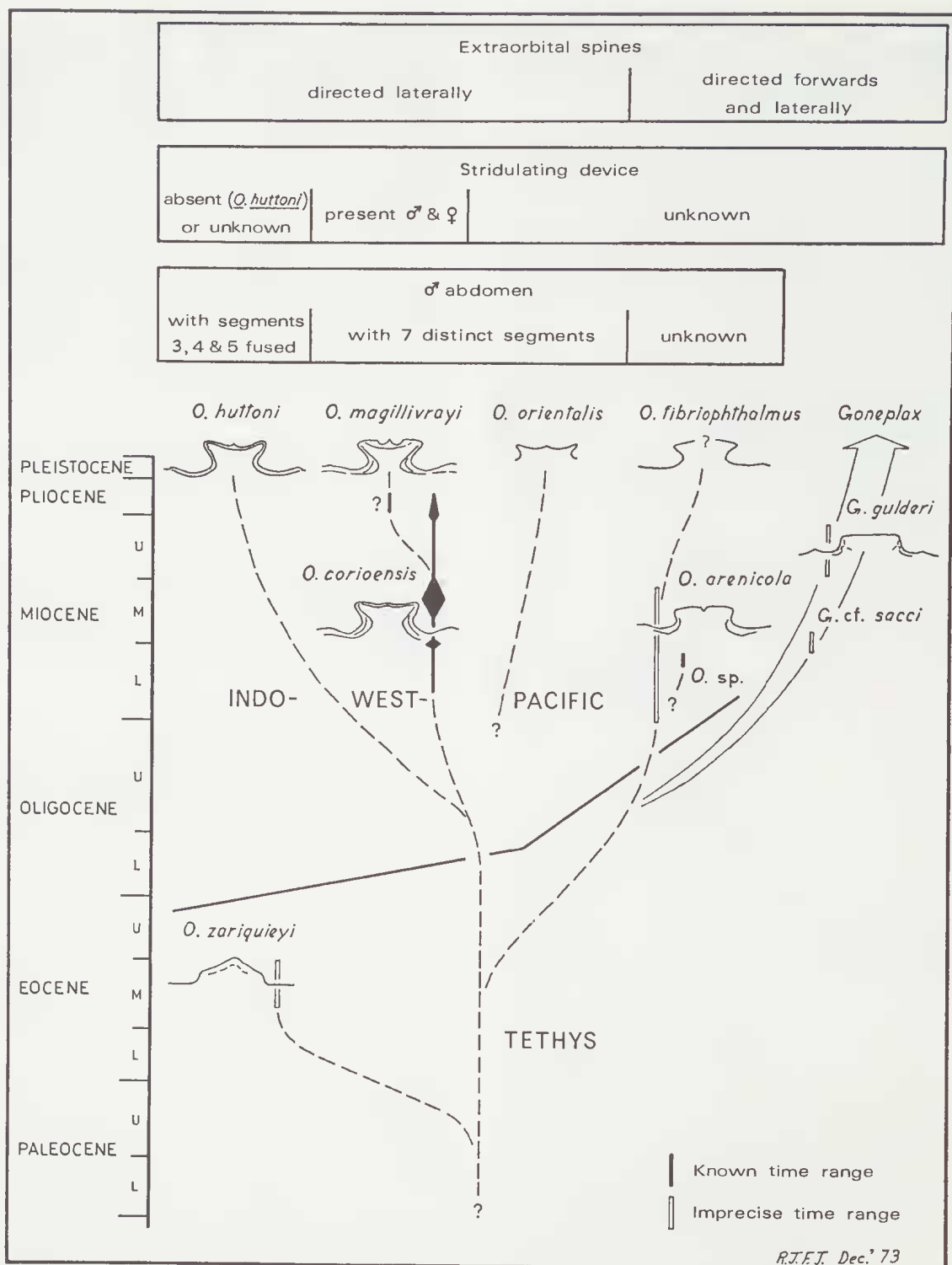
Acknowledgements

FIGURE 9

Evolutionary lineages within *Ommatocarcinus* and suggested origin of *Goneplax*. The front of most species in illustrated (*O. zariqueyi* after Vía, 1959; *O. arenicola* after Glaessner, 1960; *O. orientalis* after Tesch, 1918; *O. fibriophthalmus* after Yokoya, 1933; *G. gulderi* after Bachmayer, 1953).

comparison. Dr R. R. Lamacroft, C.S.I.R.O., programmed data for the regression analyses. The project was supported by a C.S.I.R.O. Junior Postgraduate Studentship.

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12 (1): 1-226.

Explanation of Plates

PLATE 4

Ommatocarcinus corioensis (Creswell)

Fig. 1. Lectotype, dorsal view. In a remanié phos-
phatic nodule from (the base of the Moora-
bool Viaduct Sands) Curlewis, Victoria:
N.M.V. P7665a; x 1½.

Fig. 2. Carapace, dorsal view. The hind part of the
carapace is preserved as an internal mould
which shows muscle attachment areas ad-
jacent to the anterior of the intestinal region.
From (the Port Campbell Limestone) Cur-
dies River lime works, Victoria: N.M.V.
P26118; x 1½.

Fig. 3. Internal mould of carapace, dorsal view.
Areas of muscle attachment are indicated
by a raised or reticulate ornamentation.
In a remanié phosphatic nodule from the
base of the Moorabool Viaduct Sands,
Batesford, Victoria: A.U. F17214; x 1½.

Fig. 4. Front, dorsal view. From (the Port Campbell
Limestone) Two Mile Beach, near Port
Campbell, Victoria: hypotype of Hall
(1905), ♀, N.M.V. P7668; x 3.

Fig. 5a-d. Mature male. From the Port Campbell
Limestone, notch east of the Amphitheatre,
Port Campbell: N.M.V. P24719.
a, dorsal view: x 1.
b, anterior view: x 1.
c, anterior view, enlarged. S, pterygostomial
stridulating ridge; P, plectrum on cheliped
merus. The pleural suture is broken:
x 2.
d, ventral or external view of hands: x 1.

Fig. 6. Stridulating ridge on anterior of pterygo-
stomial region. In a remanié phosphatic
nodule from the base of the Moorabool

Viaduct Sands, railway cutting at Cowies Creek, near Geelong, Victoria: A.U. F17216; x 3.

Fig. 7. Right chela of mature male. From near the top of the upper member of the Morgan Limestone at the type section, 6 km south of Morgan, South Australia: A.U. F17218; x 1.

Fig. 8. Inner sides of left fingers and right chela. From the Balcombe Clay, downstream section at Grices Creek, near Mornington, Victoria: N.M.V. P26050; x 1.

PLATE 5
Ommatocarcinus corioensis (Cresswell)

Fig. 1a,b. Mature male. From the Port Campbell Limestone, Gravel Point, near Port Campbell: N.M.V. P24721.
a, dorsal view: x 1.
b, posterior view showing the first three abdominal segments: x 1.

Fig. 2a,b. Mature male. From (the Port Campbell Limestone) Two Mile Beach, near Port Campbell: hypotype of Hall (1905), N.M.V. P7667.
a, ventral view: x 1.
b, propodi of first two legs, showing ventral lines of pits: x 2.

Fig. 3. Sub-frontal region and epistome, anterior view. From the Port Campbell Limestone, top of cliffs at Point Hesse, west of Port Campbell: ♂, N.M.V. P25989: x 3.

Fig. 4a,b. Moderate sized female. In a remanié phosphate nodule from the base of the Moorabool Viaduct Sands, 'Coghills', near Geelong: A.U. F17221.
a, third maxillipeds, ventral view. The inner margin of the right ischium and outer margin of the left ischium are damaged: x 4.
b, sternum and abdomen, ventral view: x 1¼.

Fig. 5. Sternum and abdomen of male. In a remanié phosphatic nodule from the base of the Moorabool Viaduct Sands, 'Rugby Pk.', near Fenwick, western Bellarine Peninsula, Victoria: A.U. F17219; x 1½.

Fig. 6. Moderate sized female, dorsal view. From (the Fyansford Clay) section 2B, Parish of Murgheboluc, Victoria, N.M.V. P25987; x 1.

Fig. 7. Merus of cheliped, ventral view, showing spines on the anterior and ventral margins. From (the Port Campbell Limestone) Two Mile Beach, near Port Campbell: ♀, N.M.V. P25988; x 2.

Fig. 8. Ventral view of small individual in a concretion from the Grange Burn Coquina, Forsyth's Bank, Grange Burn, near Hamilton, Victoria: N.M.V. P24689; x 2.

Fig. 9. Dorsal view of specimen from the Fossil Bluff Sandstone, Fossil Bluff, near Wynyard, Tasmania: T.U. 55357; x 1.

Fig. 10. Carapace of mature male, dorsal view. From near the top of the upper member of the Morgan Limestone at the type section, 6 km south of Morgan. A.U. F17217; x 1.

Ommatocarcinus macgillivrayi White

Fig. 11. Left cheliped palm and fragment of carpus tentaively referred to O. macgillivrayi. From the upper shell bed in the Jemmys Point Formation, road cutting on the west side of Bunga Creek, near Lakes Entrance, Victoria: N.M.V. P24686; x 1.

PLATE 6
Ommatocarcinus macgillivrayi White

Fig. 1. Holotype. From Port Curtis, Queensland. Photographs by courtesy of the British Museum of National History: ♂, 50-11, (Brit. Mus. dried coll.). Outer side of chelae at top, inner side of chelae immediately below; carapace and appendages in dorsal view.

Fig. 2. Carapace of mature male, dorsal view. From near Sydney, New South Wales: A.M. P1147; x 1.

Fig. 3. Carapace of male. Sub-fossil, from dredgings at Luggage Point, mouth of Brisbane River, Morton Bay, Queensland: Q.M. F5624; x 1.

PLATE 7
Ommatocarcinus macgillivrayi White

Fig. 1. Female, ventral view. From Sow and Pigs Shoal, Port Jackson, New South Wales: A.M. P10090; x 4/5.

Fig. 2a-e. Mature male. From near Sydney, New South Wales: A.M. P1147.
a, front, anterior view: x 2.
b, third maxillipeds, antennules and antennae, ventral view: x 2½.
c, pterygostomial stridulating ridge (S) and plectrum (P) on cheliped merus, anterior view: x 2.
d, sternum and abdomen, ventral view: x 1¼.
e, basal abdominal segments, posterior view. The carapace is slightly raised to expose the first segment: x 1¼.

Ommatocarcinus huttoni Filhol

Fig. 3a-c. Male, from off Greymouth Bar, South Island of New Zealand: D.M. Cr1765.
a, carapace, dorsal view: x 2.
b, right (upper) and left chelae, inner surfaces shown: x 1½.
c, sternum and abdomen, ventral view: x 2.

Fig. 4a,b. Female, from Cook Strait, New Zealand: D.M. Cr1171.
a, front and epistome, anterior view: x 4.
b, third maxillipeds and anterior part of pterygostomial region, ventral view: x 4.

PLATE 8

Burrows attributed to Ommatocarcinus corioensis (Cresswell) in the Port Campbell Limestone in the sea cliffs of the Port Campbell area, Victoria.

Fig. 1. Burrow complex weathering out of the bedding-plane erosion surface at the top of London Bridge, W. of Port Campbell. The hammer is 32 cm long.

Fig. 2. Speeimen of *O. corioensis* (near pen-top) preserved scemingly at the end of its burrow. Erosion surface at thc top of Gravel Point, E. of Port Campbell. The pen-top is 6 cm long.

Fig. 3. Specimen of *O. corioensis* associated with a burrow eomplex wcathering out of a bedding plane crosion surface on a eliff top near the mouth of the Sherbrook River, E. of Port Campbcll.

Fig. 4. Lateral view of burrow infilling showing the shallowly oblique, gently eurved lamination which is a frequent feature. Top of London Bridge. Bar scale equivalent to 10 cm.

Fig. 5. Burrow eomplex weathering out of a bedding-plane erosion surfaee on a eliff top near the mouth of the Sherbrook River. E, probable remnants of burrow entranee funnel.